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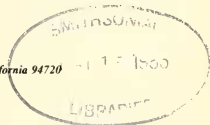
Vol. 44, No. 11, pp. 237-267, 40 figs., 2 tables.

May 6, 1986

LAND MOLLUSKS (GASTROPODA: PULMONATA) FROM
EARLY TERTIARY BOZEMAN GROUP, MONTANA

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ABSTRACT: The Bozeman Group consists of fluvial, eolian, and lacustrine rocks deposited in intermontane basins of western Montana after the Laramide Orogeny. In the Three Forks Quadrangle, three early Tertiary formations have yielded land mollusk fossils. The Milligan Creek Formation (of probable Eocene age) contains snails of the genera *Gastrocopta* (two species), *Radiocentrum*, and *Helminthoglypta*; the Climbing Arrow Formation (middle or late Eocene) contains *Gastrocopta* and *Polygyrella*; the Dunbar Creek Formation (latest Eocene or early Oligocene) contains *Gastrocopta* (two species), *Pupoides* (two species), *Radiocentrum*, and *Helminthoglypta*. Three species of *Gastrocopta*, one of *Pupoides* (*Ischnopupoides*), two of *Radiocentrum*, and one of *Helminthoglypta* are described as new. Two others (*Pupoides* and *Polygyrella*) are scarcely distinguishable from extant species.

No interregional correlations are suggested because the land mollusk faunas of the western interior are too spottily known at present. In the Bozeman Group, genera and species groups that are now allopatric occur together. The land mollusks indicate a change in terrain through time: from sparsely vegetated to forested and back again. Climates were temperate and, at least toward the end of the interval, seasonally variable.

Numerous land mollusk taxa in upper Cretaceous and Tertiary rocks of western North America occur outside the Holocene ranges of their families and genera. It is suggested that the evolutionary and biogeographic history of North American land mollusks through the Tertiary has involved (1) the sorting out of component taxa into different geographic/adaptive zones; (2) restriction of many forms to lower latitudes, concurrent with climatic cooling; and (3) eastward and westward displacements, probably related to availability of rainfall. For land mollusks, the late Eocene-early Oligocene was a time not so much of evolutionary innovation as of local extinction and biogeographic rearrangement.

INTRODUCTION

Land and freshwater mollusks from early Tertiary continental sediments of the Bozeman Group in the Three Forks Quadrangle, southwest Montana (Fig. 1), have been reported in checklists by Taylor (*in* Robinson 1963; Taylor 1975). The terrestrial gastropods were not figured or discussed taxonomically; many were not identified beyond family. However, the assemblage is an unusual one and bears strongly on the origins of present-day American land mollusk faunas. Preservation of the fossils ranges from fair to excellent. Seven species are represented by material good enough to permit description of them as new herein, and nearly all taxa can be char-

acterized in greater detail. Table 1 presents a summary of the fauna.

Robinson (1963) presented a detailed account of the geology of the Three Forks Quadrangle. He defined the Bozeman Group—which he anticipated would be recognizable on a regional scale—as the Tertiary fluvial, eolian, and lacustrine rocks that accumulated in the basins of western Montana after the Laramide Orogeny. In the Three Forks Quadrangle the group consists mainly of four formations (Fig. 2). The Sphinx Conglomerate, stratigraphically the lowest, is a limestone conglomerate probably originating as an alluvial apron; it is not fossiliferous.

Next lowest is the Milligan Creek Formation, consisting of light-colored, fine-grained, tuffa-

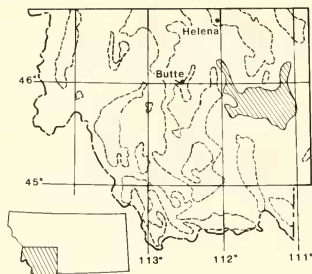


FIGURE 1. Index map of southwestern Montana. Three Forks Basin diagonally hatched; other intermontane basins stippled. After Robinson (1961).

ceous lake deposits that range from limestone to calcareous mudstone. Where it crops out, in the southwest part of the quadrangle, it produces whitish dissected benchlands. Its maximum

thickness is probably not much greater than 90 m. Fossils from the Milligan Creek Formation include five taxa of land snails, all from one locality (USGS 20007). Freshwater mollusks are evidently more widespread and are reported from five additional localities (Taylor 1975). The freshwater gastropod *Lymnaea* is also present at USGS 20007. Ostracods and charophyte remains occur in the formation. The age is probably Eocene but none of the fossils is age-diagnostic. The limestone and other fine-grained rocks of the Milligan Creek Formation were deposited in a perennial lake. Partly based on the snail here described as *Radiocentrum laevidomus*, Robinson (1963) inferred that the lake basin lay in mountainous terrain not much different from that of the present.

The Climbing Arrow Formation conformably overlies the Milligan Creek Formation in places but elsewhere may have formed contemporaneously with it. The Climbing Arrow is made up of olive, thick-bedded, sandy bentonitic clay and coarse sand, with subordinate light-colored siltstone, sandstone, conglomerate, and limestone.

TABLE 1. OCCURRENCE OF LAND MOLLUSKS IN EARLY TERTIARY BOZEMAN GROUP IN THREE FORKS QUADRANGLE, SOUTHWEST MONTANA. Locality numbers are those of U.S. Geological Survey Cenozoic Series.

Taxon	Mil- ligan Creek Forma- tion 20007	Climbing Arrow Formation		Dunbar Creek Formation						
		20008	20009	20011	20012	20013	20014	20015	20016	20017
Class Gastropoda										
Subclass Pulmonata										
Family Pupillidae										
<i>Gastrocopta (Albinula) montana</i> n. sp.	X	—	—	—	cf.	cf.	—	—	—	cf.
<i>G. (A.) sp. a</i>	X	—	—	—	—	—	—	—	—	—
<i>G. (A.) sagittaria</i> n. sp.	—	—	X	—	—	—	—	—	—	—
<i>G. cordillerae</i> n. sp.	—	—	—	—	X	X	—	X	X	X
<i>Pupoides (Ischnopupoides) tephrodes</i> n. sp.	—	—	—	—	—	X	—	X	X	—
<i>P. (I.) sp.</i> , cf. <i>P. (I.) hordaceus</i> (Gabb, 1866)	—	—	—	—	X	—	—	—	—	—
Family Oreohelicidae										
<i>Radiocentrum taylori</i> n. sp.	—	—	—	—	—	X	X	X	X	X
<i>R. laevidomus</i> n. sp.	X	—	—	—	—	—	—	—	—	—
Family Ammonitellidae										
<i>Polygyrella</i> sp., cf. <i>P. polygyrella</i> (Bland and Cooper, 1861)	—	X	X	—	—	—	—	—	—	—
Family Helminthoglyptidae										
<i>Helminthoglypta bozemanensis</i> n. sp.	—	—	?	X	—	—	—	cf.	cf.	—

It is extensively exposed in the Three Forks Quadrangle and tends to form subdued topography of low, rounded hills separated by broad, smooth valleys. The formation is not less than 220 m thick, and may be fully twice that. Two fossil localities (USGS 20008, 20009) have yielded three taxa of land snails. Freshwater gastropods are also present in the formation, including one, *Physa?*, from USGS 20009 (Taylor 1975). The Climbing Arrow Formation ranges in age from middle or late Eocene to early Oligocene. A small assemblage of vertebrates from the lower part of the formation was assigned a probable Uintan age (middle to late, but not latest, Eocene) (G. E. Lewis in Robinson 1963). Pipestone Springs (late Eocene) and Chadronian (latest Eocene to early Oligocene) vertebrates are known from higher in the formation (Hough and Lewis in Robinson 1963). A single locality well down in the lowest stratigraphic unit of the Climbing Arrow has yielded the freshwater planorbid gastropod *Biomphalaria pseudammonius* (Schlotheim), diagnostic of middle to late Eocene age and a tropical climate (McKenna et al. 1962; Taylor 1985). This locality is several hundred meters stratigraphically below the Uintan vertebrate locality. The terrestrial snail localities are probably in the Uintan rather than the Chadronian part of the formation. A diverse fossil microflora exists but has not been studied (Robinson 1963). The Climbing Arrow originated largely as the product of an aggrading stream system. The coarser sediments are stream-channel deposits; the finer-grained ones, evidently overflow deposits that accumulated on the floodplains in short-lived ponds and lakes.

The Dunbar Creek Formation, stratigraphically the highest named formation of the group, consists of white to grayish yellow thick-bedded tuffaceous siltstone, partly lacustrine and partly eolian in origin, laced with fluvial sandstone and conglomerate; minor limestone and bentonitic clay are also present. The formation is 80–240 m thick in the Three Forks Quadrangle and forms a topography much like that of the Milligan Creek—white benchlands rising steplike from the floodplain, dissected by many steep-walled canyons. The constituent sediments were evidently deposited in a more or less enclosed local basin (part of the larger Three Forks structural basin) which, at least part of the time, contained standing water. Whether the ash of a particular stratum

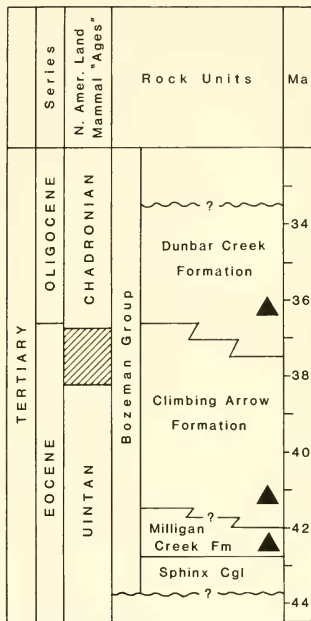


FIGURE 2. Stratigraphic and inferred temporal relations of early Tertiary formations of the Bozeman Group, Three Forks Basin, Montana. Filled triangles indicate sources of land mollusks reported in this study. Ma = millions of years before present.

fell in water or on dry land is not always easy to determine, but from the predominance of channeling by "sands and gravel derived from the neighboring highlands and containing little contemporaneous pyroclastic debris," Robinson (1963:80) concluded that if the bulk of the tuffaceous sediments were deposited in a lake, it must have been shallow and often dry. Seven sampling sites yielded a fauna of six species of terrestrial snails, while two other localities in the formation contain freshwater gastropods (Taylor

1975). Thin limestones in the Dunbar Creek Formation may be evaporites or possibly fossil caliche horizons, suggestive of bolson rather than lake conditions.

Based on the presence of brontothere and oreodont bones, Hough and Lewis (*in* Robinson 1963) assigned a Chadronian (latest Eocene to early Oligocene) age to the lower 80 m of the Dunbar Creek Formation. Vertebrate fossils and land snail remains are not recorded from identical localities, but the land snail localities are within this part of the formation. Other parts of the formation are of less certain age and regarded simply as Oligocene.

Remnant patches of middle and late Tertiary sands and gravels, too small and discontinuous to be mapped, also occur in the Three Forks Quadrangle. These are correlated with the Madison Valley beds of Douglass (1903), which elsewhere in the Three Forks Basin lie with angular unconformity on the Dunbar Creek Formation (Robinson 1961). They have yielded a variety of mammal bones, indicating Miocene and Pliocene ages, but as yet no molluscan fossils are recorded.

The unconformity within the Bozeman Group that divides lower, predominantly fine-grained, Eocene and Oligocene strata from upper, predominantly coarse-grained, Miocene and Pliocene strata is probably of regional extent. Kuenzi and Fields (1971, fig. 4) correlated similar rock sequences in the Ruby, Jefferson, Three Forks, Townsend, and Clarkston basins. A biota from the Douglass Creek Basin (Konizeski 1961) suggests time correlation with the Climbing Arrow Formation. Lillegraven and Tabrum (1983, fig. 2) presented an interbasinal correlation diagram including the Dunbar Creek and Climbing Arrow formations, but the placement of these units with reference to the radiometric time scale remains highly inferential.

LOCALITY DESCRIPTIONS

Locality numbers given are those of the U.S. Geological Survey Cenozoic series. Altitudes are given in feet as in the original locality register (with metric equivalents supplied) and are correct to ± 10 ft. All localities are in the Three Forks Quadrangle (USGS, Topographic, 1:62,500, edition of 1950), southwest Montana. Localities are plotted on map by Robinson (1963, pl. 2).

Milligan Creek Formation

20007. NW $\frac{1}{4}$ SW $\frac{1}{4}$ sec. 36, T 1 N, R 1 W; altitude 4,260 ft (1,300 m).

Climbing Arrow Formation

20008. SE $\frac{1}{4}$ NE $\frac{1}{4}$ NE $\frac{1}{4}$ sec. 11, T 2 N, R 1 W; altitude 4,600 ft (1,400 m).

20009. NE $\frac{1}{4}$ NE $\frac{1}{4}$ NE $\frac{1}{4}$ sec. 11, T 2 N, R 1 W; altitude 4,580 ft (1,400 m).

Dunbar Creek Formation

20011. SE $\frac{1}{4}$ NW $\frac{1}{4}$ sec. 6, T 2 N, R 2 E; altitude 4,360 ft (1,330 m).

20012. NW $\frac{1}{4}$ NW $\frac{1}{4}$ sec. 5, T 2 N, R 2 E; altitude 4,350 ft (1,330 m).

20013. NW $\frac{1}{4}$ SW $\frac{1}{4}$ sec. 3, T 2 N, R 1 E; altitude 4,230 ft (1,290 m).

20014. Same location as USGS 20013 but 6 m stratigraphically higher.

20015. NW $\frac{1}{4}$ SW $\frac{1}{4}$ sec. 3, T 2 N, R 1 E; altitude 4,235 ft (1,290 m).

20016. S $\frac{1}{2}$ NE $\frac{1}{4}$ SE $\frac{1}{4}$ sec. 19, T 3 N, R 1 E; altitude 4,450 ft (1,360 m).

20017. NW $\frac{1}{4}$ SW $\frac{1}{4}$ sec. 3, T 2 N, R 1 E; altitude 4,235 ft (1,290 m).

SYSTEMATIC PALEONTOLOGY

The following institutional abbreviations are used: CAS—Department of Invertebrate Zoology, California Academy of Sciences; USGS—United States Geological Survey; USNM—Division of Paleobiology, United States National Museum of Natural History, Smithsonian Institution.

Class GASTROPODA
Subclass PULMONATA
Order ORTHURETHRA
Family PUPILLIDAE

Gastrocopta Wollaston, 1878

TYPE-SPECIES: *Pupa acutus* Benson, 1856, by subsequent designation (Pilsbry 1916:18).

DIAGNOSIS.—Shell "rimate or perforate, cylindrical or ovate-conic, having the angular and parietal lamellae more or less completely united into one *biramose, bifid, lobed or sinuately lamella* (or rarely the angular is wanting). Columellar lamella present; palatal folds present . . . ; lip well expanded" (Pilsbry 1948:871).

REMARKS.—*Gastrocopta* is the most widely distributed genus of the Pupillidae, with a recorded stratigraphic range of Eocene to Recent (Pilsbry 1948; Zilch 1959; Preece 1982). Pilsbry distinguished two main geographic groups—a northern, and a tropical and southern continent series—each with several subgenera. The subgenus *Albinula* Sterki, 1892, is part of the northern group.

The "*Gastrocopta?* sp." reported by La Rocque (1960) from the Flagstaff Formation. Paleocene of Utah, does not show sufficient detail for assignment to a subgenus. If correctly allocated to *Gastrocopta*, it is the oldest known member of the genus. Taylor (1975) reported an undescribed species of *Gastrocopta* (*Gastrocopta*) from the Tepee Trail (=Wagon Bed) Formation, upper Eocene of Wyoming, and other fossils questionably referred to *Gastrocopta* from the Wagon Bed and White River formations (lower Oligocene), Wyoming. Pilsbry (1916–18) noted that the Oligocene and Miocene species of Europe seem "a little too specialized" to have been ancestral to the American species. It is reasonable therefore to expect ancestral forms in Eocene, Paleocene, and perhaps upper Cretaceous strata in America and elsewhere.

(*Albinula*) Sterki, 1892

TYPE-SPECIES: *Pupa contracta* Say, 1822, by original designation.

DIAGNOSIS.—"Whitish-translucent gastrocopts having the inner end of the parietal lamella curved towards the periphery; angular lamella well developed, concrescent in varying degree with the parietal; the palatal folds stand upon a white palatal callus, and a suprapalatal fold is usually developed. Except in *G. armifera*, the columellar lamella is horizontal in front and curves toward the base within. The lip is thin and expanded" (Pilsbry 1948:874).

REMARKS.—*Albinula* occurs in the Eocene of England, the middle Oligocene through upper Miocene of Germany, the Miocene and Pliocene of France, and the Pliocene of Italy (Pilsbry 1916–18; Preece 1982). It is widespread at present in North America, although absent from the Pacific slope, but there are no other American fossil records earlier than Pliocene. The Three Forks Quadrangle is just within the western edge of the Holocene range of the subgenus. *Gastrocopta* (*Al-*

binula) *holzingeri* (Sterki, 1889) is reported to range west to Helena, Montana (Pilsbry 1948).

Several species of the subgenus, *G. armifera* (Say, 1821), *G. contracta* (Say, 1822), *G. holzingeri*, *G. falcis* Leonard, 1946, *G. proarmifera* Leonard, 1946, and *G. tridentata* (Leonard, 1946), occur in Pliocene and early Pleistocene faunas in Kansas (Franzen and Leonard 1947; Leonard 1950; Taylor 1960). *Gastrocopta armifera* also occurs in late Pleistocene deposits in Kansas and Arizona (Franzen and Leonard 1947; Bequaert and Miller 1973), and *G. contracta* occurs in Quaternary deposits in west Texas (Albritton and Bryan 1939).

Gastrocopta (*Albinula*) *montana* new species

(Figure 3)

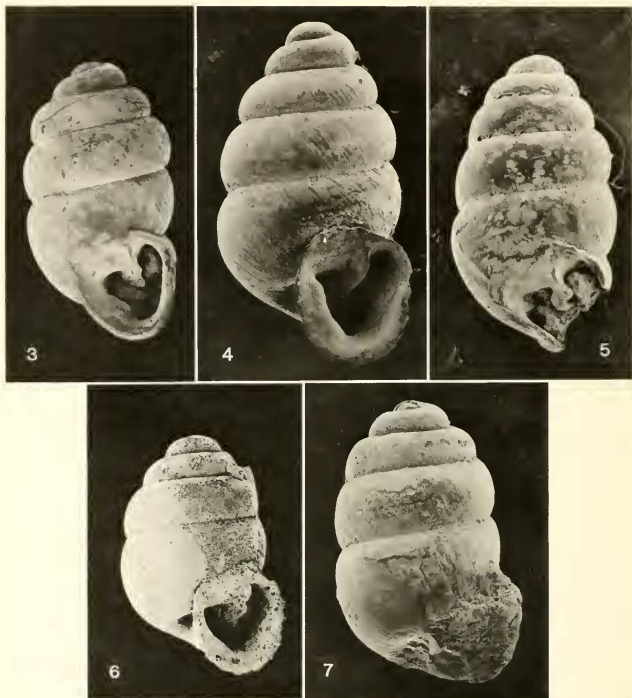
Pupillidae C. D. W. Taylor in Robinson 1963:68, table 4 (in part).—Taylor 1975:206 (non p. 209).

Pupillidae D. D. W. Taylor in Robinson 1963:68, table 4.—Taylor 1975:206.

DIAGNOSIS.—A cylindrical-ovate *Gastrocopta* (*Albinula*) with sinuous, unbranched angular lamella, sulcate body whorl, strong crest, and low callus ridges inside inner and outer lips.

DESCRIPTION.—Shell dextral, umbilicate, cylindrical-ovate, of about 5.25 whorls; suture lightly to moderately impressed, early whorls strongly convex, later ones less so. Nuclear whorls smooth; neanic sculpture of oblique growth lines, strongest just anterior to suture. Body whorl narrowly, roundly shouldered anterior to suture, compressed at periphery, attenuated toward base, sulcate behind aperture; last 0.3 whorl nearly straight in basal view, then angling toward umbilicus just behind peristome. Strong crest present behind aperture. Aperture rounded-triangular; peristome broadly reflected, thickened within by callus, limbs connected by thin callus film across face of body whorl. Outer lip sinuous, most produced medially, outer-posterior quadrant retractive. With prominent, sinuous, angular lamella, projecting not quite as far as plane of aperture, inner end thickened along axial side and deflected toward periphery. Low callus barriers present inside inner and outer lips, inner one bearing two faint denticles. Dimensions of holotype: height 2.0 mm, diameter 1.1 mm, whorls 5.2.

TYPE-MATERIAL.—Holotype: USNM 377373, from U.S. Geological Survey Cenozoic Locality 20007, Montana: Gallatin County: NW¼ SW¼ sec. 36, T 1 N, R 1 W, Three Forks



FIGURES 3-7: Figure 3. *Gastrocopta (Albinula) montana*, new species, holotype, USNM 377373; height 2.0 mm. Figure 4. *Gastrocopta (Albinula) contracta* (Say), CAS 046506; height 2.4 mm; Holocene, Lee County, Texas. Figure 5. *Gastrocopta (Albinula)* species *a*, USNM 377375; height 2.75 mm. Figure 6. *Gastrocopta (Albinula) sagittaria*, new species, holotype, USNM 377376; height 1.9 mm. Figure 7. *Gastrocopta cordilleræ*, new species, holotype, USNM 377378; height 1.8 mm.

Quadrangle (1950) 1:62,500; altitude 4,260 ft (1,300 m). Miligan Creek Formation, Eocene (?). Two paratypes, USNM 377374, from same locality as holotype.

REFERRED MATERIAL (all, *Gastrocopta* sp., cf. *G. montana*).—Dunbar Creek Formation: USGS 20012, two specimens. USGS 20013, two specimens. USGS 20017, one specimen.

REMARKS.—The type-lot consists of well-pre-

served original shells filled with colorless calcite matrix. The holotype is an adult shell. One paratype is an adult shell with reflected peristome, height 2.1 mm, diameter 1.1 mm, with 5.3 whorls. The other paratype lacks the adult peristome; dimensions: height 2.1 mm, diameter 1.1 mm, with 5.0 whorls.

Gastrocopta montana is distinguished from *Gastrocopta (Albinula)* species *a*, next described, of the Milligan Creek Formation by its smaller size, more cylindrical shape, and low callus ridges thickening the inner and outer lips internally. The base of the body whorl of *Gastrocopta (Albinula)* species *a* is more strongly compressed, almost forming a keel around the umbilicus. *Gastrocopta sagittaria* of the Climbing Arrow Formation is more conic in shape, having a broad rather than narrowed anterior end.

Material from the Dunbar Creek Formation (USGS 20012, 20013, 20017) is provisionally referred to the species. Most of the shells are slightly more cylindrical than the type-lot of *G. montana*, but one of two specimens from USGS 20012 is as broadly ovate as the types. The specimens from USGS 20013 are internal molds of tuffaceous siltstone with very little shell remaining. They show the impressions of upper and lower palatal barriers a short distance behind the position of the crest. The lower barrier is larger and more deeply immersed than the upper. The better-preserved specimen from USGS 20012 consists of original shell, partly filled with recalcitrant siltstone matrix that obscures most of the apertural dentition, but a strong, unbranched angular lamella is present, projecting almost as far as the plane of the aperture. The peristome is everted; the outer lip is sinuous, most produced medially.

The Pliocene to Holocene *G. contracta* (Say, 1822) (Fig. 4), type-species of the subgenus *Albinula*, is the modern species most similar to *G. montana*, in its sinuous, unbranched angular lamella, strong crest, and callus ridges inside the inner and outer lips. *Gastrocopta contracta* is conic rather than cylindrical, with the penultimate whorl substantially broader than the antepenult; however, the basal configuration of the last whorl is quite similar. *Gastrocopta holzingeri* (Sterki, 1889), Pliocene to Holocene, is similar in shape to *G. montana* but has a forked, lambda-shaped angulo-parietal lamella. *Gastrocopta (Gastrocopta) cristata* (Pilsbry and Vanatta, 1900) is similar in shape and also has a distinct crest, but its angular lamella is smaller and does not turn to the right within; there is no toothed callus ridge paralleling the inner lip.

Along with English Eocene species (Preece 1982), this and the following species probably constitute the oldest known occurrence of the

subgenus *Albinula*, but as noted in the introduction the exact age of the Milligan Creek Formation is not well established.

Gastrocopta (Albinula) species *a*

(Figure 5)

Pupillidae A, D. W. Taylor in Robinson 1963:68, table 4.—Taylor 1975:206.

Pupillidae B, D. W. Taylor in Robinson 1963:68, table 4 (in part).—Taylor 1975:206 (non p. 209).

DESCRIPTION.—Shell dextral, umbilicate, ovate to elongate-ovate, of 5.2–5.5 whorls, suture moderately to deeply impressed, spire profile convex, fourth and fifth whorls about equally broad. Sculpture of fine, oblique growth lines and a trace of puckering anterior to the suture. Body whorl compressed anteriorly, sulcate behind aperture, very much narrowed toward base; last 0.3 whorl nearly straight in basal view, cross section triangular, the anterior vertex slightly pinched off on either side. Umbilicus wide, excavated. Faint crest behind aperture. Aperture ovate-triangular; peristome everted, thin, continuous, appressed to body whorl. With prominent, strongly sinuous, angular lamella, projecting as far as plane of aperture, inner end thickened and deflected toward periphery. Columellar lamella horizontal. Peglike upper and lower palatal folds sometimes present inside aperture.

REFERRED MATERIAL.—Milligan Creek Formation: USGS 20007, five specimens.

REMARKS.—The specimens at hand, while not good enough for formal taxonomic description, demonstrate that a second species of *Gastrocopta (Albinula)*, distinct from *G. montana*, occurs in the Milligan Creek Formation. The material consists of one adult shell, height 2.75 mm, diameter 1.6 mm, with 5.5 whorls (outer lip broken in manipulation); two other adults 2.3 mm in height and 1.4 mm in diameter with 5.2 whorls; an intact juvenile shell of four whorls, height 1.4 mm; and a fragment of spire (4+ whorls) about 2 mm in height. Original shell is present in all, showing fine surface incremental lines. The palatal folds present in the largest specimen are not borne on a palatal callus but arise separately within the aperture. No palatal folds are detectable on the two smaller adult shells. Otherwise the dentition is basically similar to the modern *G. contracta* (Say). The first bend in the angular lamella points toward the middle of the outer lip

at about the level of the upper palatal fold. Variation of 0.4–0.5 mm in height and 0.25–0.5 whorl in adult shells is not uncommon in modern species of *Gastrocopta* (Pilsbry 1948).

Gastrocopta montana of the Milligan Creek Formation is smaller, more cylindrical, with callus ridges thickening the inner and outer lips. *Gastrocopta sagittaria* of the Climbing Arrow Formation is also smaller and more conic in shape, having a broad rather than narrowed anterior end.

This species and *G. montana* both seem more closely related to *G. contracta* than to any other modern species; *G. contracta* may be the surviving member of a once more diversified lineage.

Gastrocopta (Albinula) sagittaria new species

(Figure 6)

Pupillidae E. D. W. Taylor in Robinson 1963:68, table 4.—Taylor 1975:208.

DIAGNOSIS.—A small, ovate-conic *Gastrocopta* with prominent, sinuous, unbranched angular lamella, broadly rounded, perforate base, and low, untoothed callus ridges inside inner and outer lips.

DESCRIPTION.—Shell small for the genus, dextral, umbilicate, ovate-conic, of 4.5–4.8 whorls; suture moderately impressed, spire profile convex, body whorl not much broader than penult. Sculpture of oblique growth lines. Body whorl either narrowly shouldered or compressed below suture, well rounded toward base; last 0.5 whorl nearly straight in basal view, laterally compressed and narrowed anteriorly into a triangular cross section. Moderately strong crest behind aperture. Aperture subquadrate; peristome everted, solid, continuous, appressed to body whorl; with low callus barriers inside inner and outer lips. With prominent, sinuous, angular lamella, projecting as far as plane of aperture, its inner end broadening to a flange extending toward periphery. Dimensions of holotype: height 1.9 mm, diameter 1.3 mm, whorls 4.8.

TYPE-MATERIAL.—Holotype: USNM 377376, from U.S. Geological Survey Cenozoic Locality 20009, Montana: Jefferson County: NE¼ NE¼ NE¼ sec. 11, T 2 N, R 1 W, Three Forks Quadrangle (1950) 1:62,500; altitude 4,580 ft (1,400 m), Climbing Arrow Formation, Eocene. Fourteen paratypes, USNM 377377, from same locality as holotype.

REMARKS.—The material consists of internal molds and thoroughly recrystallized shells, of pink to colorless calcite. Even in those specimens that

preserve the shape of the aperture and the prominent angular lamella, calcite fills the aperture to an extent that conceals the presence or absence of other lamellae or deep-seated folds. When specimens are immersed in toluene (refractive index 1.49693), it can be seen that the angular lamella first curves toward the outer lip, then recurves toward the axis. Its inner end broadens and bears a rounded flange extending toward the periphery, much as in *G. contracta* (Say).

The three most complete paratypes measure

Locality	Height	Diameter	No. of whorls
USGS 20009	1.9 mm	1.3 mm	4.7
	1.8	1.3	4.6
	1.8	1.3	4.5

Measurements include the expanded portion of the peristome.

Several younger species of *Albinula* have a similar, ovate-conic shape, including *Gastrocopta (Albinula) dupuyi* (Michaud, 1855), Pliocene of France, and the Pleistocene to Recent North American *G. contracta*. The broad, perforate base and the presence of fewer than five whorls distinguish this from any other species of *Gastrocopta* in the Bozeman Group.

The species is named for the Climbing Arrow (Latin, *sagitta*) Formation.

Subgenus indeterminate

Gastrocopta cordillerae new species

(Figure 7)

Pupillidae B. D. W. Taylor in Robinson 1963:68, table 4 (in part).—Taylor 1975:209 (*non p.* 206).

Pupillidae F. D. W. Taylor in Robinson 1963:68, table 4 (in part).—Taylor 1975:209 (in part).

Pupillidae I. D. W. Taylor in Robinson 1963:68, table 4 (in part).—Taylor 1975:209 (in part).

Pupillidae indet., D. W. Taylor in Robinson 1963:68, table 4.—Taylor 1975:209.

DIAGNOSIS.—An ovate-oblong *Gastrocopta* with short spire whorls but moderately tall body whorl, flattened or weakly sulcate behind aperture, narrowed base, small aperture, and strong to moderate crest.

DESCRIPTION.—Shell dextral, umbilicate, ovate-oblong with obtusely conic summit, of about 5.0–5.5 whorls; suture moderately impressed, whorls of spire short, convex. Nuclear whorls 1.4, smooth. First neanic whorl smooth; thereafter with sculpture of fine, markedly oblique growth lines, strongest just anterior to suture. Body whorl moderately tall, compressed, nar-

rowed toward base, flattened or weakly sulcate behind aperture, with a strong to moderate crest. Aperture small, rounded-triangular. Upper and lower palatal barriers present, discrete; rest of apertural dentition not known. Dimensions of holotype: height 1.8 mm, diameter 1.1 mm, whorls 5.1.

TYPE-MATERIAL.—Holotype: USNM 377378, from U.S. Geological Survey Cenozoic Locality 20015, Montana: Broadwater County: NW¼ SW¼ sec. 3, T 2 N, R 1 E, Three Forks Quadrangle (1950) 1:62,500; altitude 4,235 ft (1,290 m). Dunbar Creek Formation, Eocene or Oligocene. Thirteen paratypes, USNM 377379, from same locality as holotype.

REFERRED MATERIAL.—Dunbar Creek Formation: USGS 20012, one specimen, juvenile. USGS 20013, three specimens. USGS 20016, one specimen, a calcitic internal mold with little shell remaining. USGS 20017, one specimen.

REMARKS.—The holotype and paratypes consist of moderately well preserved original shells filled with grayish yellow tuffaceous siltstone. No specimen in either the type-lot or the referred material shows fully the characteristics of the aperture, and for this reason it is not possible to assign the species to a subgenus. However, it is a characteristic species of the Dunbar Creek Formation, occurring at five out of the seven localities that yielded land snails, and is readily recognized by its ovate-oblong profile and the contrast between the short whorls of the spire and the relatively tall body whorl.

On the juvenile specimen from USGS 20012, axial ribs extend across the flat base but are much weaker than those above the peripheral angulation. The largest paratype is 2.4 mm long and 1.3 mm in diameter without having the complete aperture present. A referred specimen from USGS 20013 is 2.2 mm long, 1.3 mm in diameter, and ovate in outline, the base distinctly compressed; it shows a narrow angular lamella.

Pupoides Pfeiffer, 1854

TYPE-SPECIES: *Bulimus nitidulus* Pfeiffer, 1839, by subsequent designation (Kobelt 1880 [1876–81]).

DIAGNOSIS.—Shell “about 3 to 6 mm long, rimate; long-ovate, turrated or rarely cylindrical, with obtuse apex and few (generally 5–6) rather long whorls. Aperture ovate, toothless except for a small, tuberculiform angular lamella close to the insertion of the outer lip, or united with it, sometimes wanting; peristome expanded, reflected and usually thickened within. Internal axis slender, perforate” (Pilsbry 1948:920).

REMARKS.—*Pupoides* is mainly a tropical and subtropical genus, distributed on all continents except Europe; it is also absent from Southeast Asia and the East Indies. Pilsbry (1920–21) associated it with arid regions and relatively dry stations in humid areas.

Pilsbry (1922–26:249, 265) placed *Pupa incolata* White, 1876, from the Eocene of southwestern Wyoming, in *Pupoides*, but also included it in a list of Pupillidae of uncertain affinities. The figures by White (1883, pl. 29, fig. 15–17) show a conical shell with an externally thickened outer lip, doubtfully pupillid in my opinion.

(*Ischnopupoides*) Pilsbry, 1926

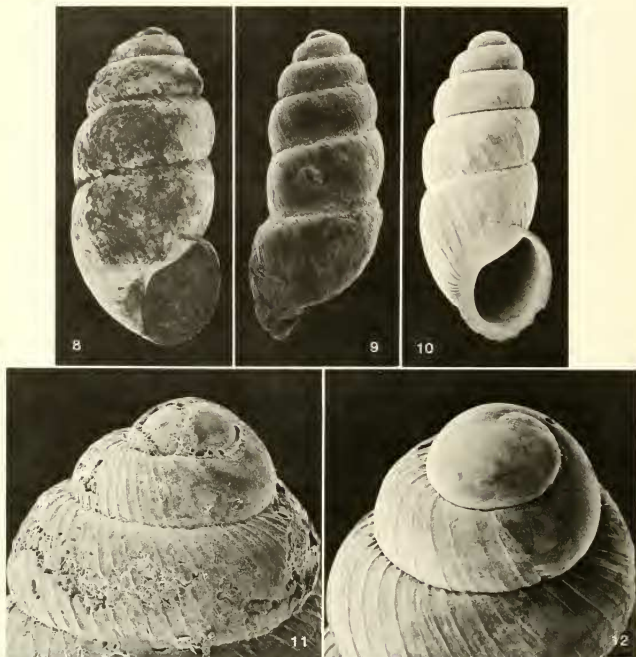
TYPE-SPECIES: *Pupa hordacea* Gabb, 1866, by original designation.

DIAGNOSIS.—“Shell cylindrical or subcylindrical; diameter decidedly less than half the length” (Pilsbry 1948:921).

REMARKS.—*Ischnopupoides* is a New World group with two closely related species living north of Mexico. *Pupoides* (*Ischnopupoides*) *hordacea* (Gabb, 1866) occurs today in Wyoming, Colorado, Kansas, Utah, Arizona, and New Mexico (Pilsbry 1948; Bequaert and Miller 1973). It is recorded from late Pleistocene or early Holocene deposits in Kansas, Texas, New Mexico, and Arizona (Bequaert and Miller 1973). *Pupoides* (*Ischnopupoides*) *inornatus* Vanatta, 1915, ranges from South Dakota to New Mexico, although as pointed out by Taylor (1960), it is documented to be living at only two localities; it also occurs in Blancan (late Pliocene and early Pleistocene) faunas in Nebraska, Kansas, and Texas. Other species referred to the subgenus occur in Mexico, Ecuador, Peru, Bolivia, Argentina, and Chile (Bequaert and Miller 1973). There are no previous records of *Ischnopupoides* in Montana.

Taylor (1975:430) reported an unnamed *Pupoides* (*Ischnopupoides*) species from the Tepee Trail (=Wagon Bed) Formation, upper Eocene of Wyoming, as follows: “one well-preserved internal mold shows the features of shape, size, apertural thickening, reflected peristome and lack of apertural lamellae. In diameter of shell and general proportions of aperture, the specimen agrees well with *P. (I.) inornatus* Vanatta, but its whorls are lower and hence total shell length is less in the fossil.”

In the following new species, *P. tephrodes*, diameter is approximately half the length (or height)



FIGURES 8-12: Figure 8. *Pupoides (Ischnopupoides) tephrodes*, new species, holotype, USNM 377380; height 3.0 mm. Figure 9. *Pupoides (Ischnopupoides) sp.*, cf. *P. (I.) hordaceus* (Gabb), USNM 377382; height 3.0 mm. Figure 10. *Pupoides (Ischnopupoides) hordaceus* (Gabb), CAS 046507; height 3.4 mm; Holocene, drift of Chaco River at Pueblo Bonito, Chaco Canyon National Monument, San Juan County, New Mexico. Figure 11. *Pupoides tephrodes* detail of apex of holotype showing transition from smooth nuclear to ribbed neanic whorls. Figure 12. *Pupoides hordaceus*, detail of apex of CAS 046507.

of the shell. This leaves little but the cylindrical form, absence of apertural tubercles, and (in some species) the presence of fine axial riblets to distinguish the subgenus. Miller (in Bequaert and Miller 1973) found that the anatomy of *P. hordaceus* differed only in minor details from that of *Pupoides (Pupoides) albilabris* (C. B. Adams, 1841). Nevertheless, the presence in the Bozeman Group of *P. tephrodes* and another species hardly distinguishable from *P. hordaceus* points

to the existence in the eastern Cordillera of a lineage distinct from *Pupoides*, *sensu stricto*, since at least Oligocene time.

***Pupoides (Ischnopupoides) tephrodes* new species**
(Figures 8, 11)

Pupillidae C. D. W. Taylor in Robinson 1963:68, table 4 (in part).—Taylor 1975:209 (in part) (*non p.* 206).
Pupillidae F. D. W. Taylor in Robinson 1963:68, table 4 (in part).—Taylor 1975:209 (in part).

DIAGNOSIS.—A small, cylindrical *Pupoides* (*Ischnopupoides*) with diameter equal to about half of height, sculpture of slender, well-spaced, retractive riblets, and peristome narrowly everted.

DESCRIPTION.—Shell dextral, narrowly umbilicate, cylindrical with convexly low-conic summit, of about 5.2 tall whorls; suture moderately impressed, crenulated by axial riblets. Early whorls convex; fourth and fifth whorls roundly shouldered below suture, compressed at periphery and anteriorly. Nuclear whorls 1.5, smooth; neanic sculpture of slender, well-spaced, retractive riblets. Body whorl narrowly, slopingly shouldered, compressed at periphery, slightly attenuated toward base, rising gently on penult behind aperture. Aperture oblique, ovate; peristome narrowly everted, not thickened within; parietal margin oblique, covered by a thin callus. No angular tubercle present. Dimensions of holotype: height 3.0 mm, diameter 1.5 mm, whorls 5.3.

TYPE-MATERIAL.—Holotype: USNM 377380, from U.S. Geological Survey Cenozoic Locality 20015, Montana: Broadwater County: NW¼ SW¼ sec. 3, T 2 N, R 1 E, Three Forks Quadrangle (1950) 1:62,500; altitude 4,235 ft (1,290 m). Dunbar Creek Formation, Eocene or Oligocene. Two paratypes, USNM 377381, from same locality as holotype.

REFERRED MATERIAL.—Dunbar Creek Formation: USGS 20013, three specimens, internal molds. USGS 20016, three specimens, internal molds with some shell preserved, showing fine oblique riblets.

REMARKS.—The type-lot consists of moderately well preserved original shells filled with grayish yellow tuffaceous siltstone. The axial riblets are worn on all specimens so that in places they are visible only near the suture; similar wear occurs in Recent species of *Pupoides* (*Ischnopupoides*). One paratype measures: height 2.8 mm, diameter 1.3 mm, with 5.2 whorls. The other paratype measures: height 2.7 mm, diameter 1.2 mm, with 5.1 whorls. Diameter/height ratios for intact material range from 0.44–0.50, compared to a range of 0.40–0.45 for *P. hordaceus* and 0.44–0.46 for *P. inornatus* (calculated from dimensions given by Pilsbry [1948]).

The shells are smaller than in either *P. hordaceus* or *P. inornatus*, both of which may exceed 3.5 mm in length. The peristome is less sharply turned out. The rather tall, loosely coiled whorls (parietal wall encroaching little upon the aperture) and the cylindrical outline are wholly typical of the subgenus *Ischnopupoides*.

The name *tephrodes* combines the Greek *tephra*, ash, with the suffix *-odes*, denoting fullness.

Pupoides (Ischnopupoides) sp.,
cf. *P. (I.) hordaceus* (Gabb, 1866)

(Figure 9)

Pupillidae C. D. W. Taylor in Robinson 1963:68, table 4 (in part).—Taylor 1975:209 (in part) (*non p.* 206).

DESCRIPTION.—Shell dextral, narrowly umbilicate, cylindrical with convexly conic summit, of 5.1–5.5 tall whorls; suture not deeply impressed. Early whorls convex; fourth and fifth whorls roundly shouldered below suture, compressed at periphery and anteriorly. Nuclear whorls 1.4, smooth; neanic sculpture of faint, slender, irregularly spaced, retractive riblets. Body whorl elongate, smoothly rounding toward base, rising slightly on penult behind aperture. Aperture ovate; parietal margin sinuous, not strongly encroaching on aperture; peristome broken on all specimens at hand.

REFERRED MATERIAL.—Dunbar Creek Formation: USGS 20012, five specimens.

REMARKS.—The material consists of recrystallized shells with filling of cream-colored tuffaceous siltstone. Although the peristome is not preserved in any of the specimens at hand, the shape of the shell is almost identical to Holocene *P. hordaceus* (Fig. 10, 12). The surface of the fossils is somewhat worn, so the original strength of the axial ribbing cannot be evaluated. The strongest riblets seem to have been more irregularly spaced than those of *P. hordaceus*. Better-preserved material would also show whether the ribbing was stronger than that of *P. inornatus* Vanatta.

The four most nearly intact specimens measure

Locality	Height	Diameter	No. of whorls
USGS 20012	3.2 mm	1.2 mm*	5.5
	3.1	1.3	5.4
	3.0	1.3	5.5
	3.0	1.4	5.1

* Broken.

These specimens differ from *P. tephrodes* in being slimmer and less distinctly ribbed, and in having a more steeply conical summit.

Order SIGMURETHRA
Family OREOHELICIDAE

Radiocentrum Pilsbry, 1905

TYPE-SPECIES: *Oreohelix chiricahuana* Pilsbry, 1905, by original designation.



FIGURES 13-15. *Radiocentrum hendersoni* (Russell), holotype, USNM 497659; diameter 7.8 mm.

DIAGNOSIS.—Oreohelicids with "embryonic shell of about $1\frac{1}{2}$ radially ribbed whorls; penis club-shaped, the walls of its cavity plain in the anterior part, having oblique ridges irregularly en chevron in the middle and posterior parts, wide and truncate at the end, epiphallus about as long as the penis, slender anteriorly, the penial retractor inserted on it a short distance from its entrance in the penis. Reproduction oviparous" (Pilsbry 1939:540). Babrakzai et al. (1975) found a large number of submetacentric chromosomes and a haploid chromosome number of 32 to be characteristic of *Radiocentrum*.

The few-whorled, radially costulate protoconch is the only paleontologically useful diagnostic character, but it is adequate for recognition of this group. The shells are otherwise much like *Oreohelix*, depressed-helicoid to lenticular in shape, the periphery ranging from rounded, through obtusely subangular, to distinctly carinate.

REMARKS.—The endemic North American pulmonate family Oreohelicidae consists of two genera: *Oreohelix* Pilsbry, 1905, and *Radiocentrum*, the latter originally proposed as a subgenus of the former.

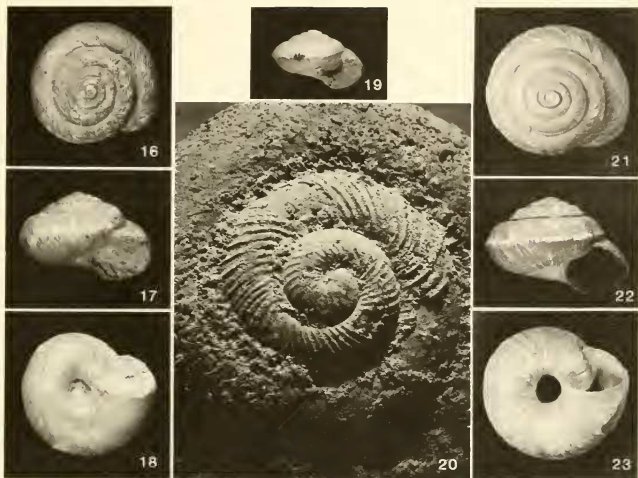
Conchologically, *Radiocentrum* has a distinctive, radially ribbed 1.5-whorled embryonic shell. Living *Radiocentrum* deposit eggs, whereas Recent *Oreohelix* are ovoviviparous. On reproductive characters and chromosome data, Babrakzai et al. (1975) elevated *Radiocentrum* to generic status.

The modern distribution of *Radiocentrum* includes southern New Mexico, southern Arizona, trans-Pecos Texas (late Pleistocene; Metcalf and Johnson 1971), northern Coahuila (probable late

Pleistocene; Metcalf 1980), Chihuahua, Baja California Sur (Miller 1973a; Christensen and Miller 1976), and Santa Catalina Island off southern California (Hochberg et al., in press).

Tozer (1956) found *Oreohelix angulifera* (Whiteaves, 1885) from the St. Mary River and Edmonton formations, upper Cretaceous of western Alberta, and *Oreohelix thurstoni* (Russell, 1926) from the Paskapoo, Porcupine Hills, and Willow Creek formations, Paleocene of western Alberta, to have regular costae on the embryonic whorls, strongly suggestive of *Radiocentrum*. Additional fossil oreohelicids probably assignable to *Radiocentrum* include *R. grangeri* (Cockerell and Henderson, 1912) from the Eocene of Park County, Wyoming, and *R. hendersoni* (Russell, 1938) from the Oligocene of Colorado. The latter was originally described in the genus *Gonyodiscus* Fitzinger, 1833 (Discidae), but is here reassigned to *Radiocentrum* based upon examination of photographs of the holotype (USNM 497659) (Fig. 13-15), supplied by D. W. Taylor. Sculpture of the protoconch is not preserved, but the whorl diameter increases suddenly after 1.5 whorls, as it does at the beginning of neanic growth in many *Radiocentrum*. *Helix nacimientensis* White, 1886, from the Paleocene of New Mexico, assigned to *Radiocentrum* by Cockerell (1914), is probably not an oreohelicid snail and may belong to the Helminthoglyptidae (Taylor 1975).

Cretaceous and Tertiary species of *Radiocentrum* are all from north of the present range of the genus, along the eastern Cordillera. The genus has undergone a southward restriction or displacement of range since Paleogene time; the Pleistocene and Holocene range includes disjunctions probably related to the late Cenozoic



FIGURES 16-23: Figures 16-20. *Radiocentrum taylori*, new species. Figures 16-18, holotype, USNM 377383; diameter 12.4 mm. Figure 19, paratype, USNM 377384; diameter 8.1 mm. Figure 20, referred specimen, USNM 377386; detail of apical sculpture, $\times 35$. Figures 21-23. *Radiocentrum chrichahuanum obsoletum* (Pilsbry and Ferriss), CAS 046508; diameter 12.6 mm; Holocene, Whitetail Canyon, Chrichahua Mountains, Cochise County, Arizona. All specimens coated for photographing.

emergence of the Sonoran and Chihuahuan deserts as arid environments of regional extent (Hochberg et al., in press).

The type localities of the two new species of *Radiocentrum* described here are approximately 1,600 km north of the northernmost Holocene occurrences of the genus. The present distribution of *Radiocentrum* consists of scattered, highly local enclaves. Taken together, the fossil and Recent range data suggest restriction from a formerly more widespread and continuous range that included the northeastern Cordillera. *Radiocentrum* has been distinct from *Oreohelix* since at least the late Cretaceous; species of *Oreohelix* are known from upper Cretaceous, Paleocene, and Eocene strata from Alberta to Utah (Pilsbry 1939; Tozer 1956; La Rocque 1960). No other generic groups are recognized in the family. In contrast to the Helminthoglyptidae of the arid Southwest, which have responded to fragmen-

tation of range and isolation by a dramatic, evidently saltational, generic diversification (Miller 1973*b*, 1981*a*), the Oreohelicidae have been evolutionarily conservative.

Radiocentrum taylori new species

(Figures 16-20)

Oreohelix n. sp., D. W. Taylor in Robinson 1963:68, table 4 (in part).—Taylor 1975:209.

DIAGNOSIS.—A small, solid, low-trochoid *Radiocentrum* of about 5.25 whorls; periphery angulate to obtusely keeled; protoconch strongly radially ribbed, ribs overhanging abaperturally; neanic sculpture of irregular ribs, lightly decussated on base by incised spirals.

DESCRIPTION.—Shell low-trochoid, solid, height about 0.65 times diameter, apical angle 124° . Whorls about 5.25; spire profile weakly convex; suture not deeply impressed. Body whorl

slightly shouldered, about equally convex above and below periphery, not markedly descending except immediately behind aperture. Periphery angulate to obtusely keeled (particularly on last 0.5 turn). Aperture circular, at about 40° angle to axis of coiling; limbs of peristome approaching closely, parietal wall with thin wash of callus; peristome not expanded but inner lip reflected toward umbilicus. Base well rounded, umbilicus contained about six times in diameter of shell. Protoconch consisting of 1.5 whorls, nuclear tip smooth, thereafter with prominent, elevated radial ribs, slightly convex-forward, overhanging on abapertural side, and almost as wide at the interspaces between. End of protoconch sometimes slightly thickened; onset of neanic growth marked by abrupt increase in whorl diameter and/or change in obliquity of radial ribs. Ribs of neanic shell at first upstanding and bladellike, quickly becoming lower, more solid, and less regularly spaced. Ribbing on body whorl crude, slightly sinuous over periphery, and lightly decussated by fine spiral striae particularly evident on base and on shoulder of last 0.25 whorl. Dimensions of holotype: diameter 12.4 mm, height 7.9 mm, whorls 5.3.

TYPE-MATERIAL.—Holotype: USNM 377383, from U.S. Geological Survey Cenozoic Locality 20015, Montana: Broadwater County: NW¼ SW¼ sec. 3, T 2 N, R 1 E, Three Forks Quadrangle (1950) 1:62,500; altitude 4,235 feet (1,290 m). Dunbar Creek Formation, Eocene or Oligocene. Figured paratype, USNM 377384; 39 additional paratypes, USNM 377385, from same locality as holotype.

REFERRED MATERIAL.—Dunbar Creek Formation: USGS 20013, nine specimens—three external molds of spires (the largest 12.0 mm in diameter, with 5.0 whorls) with clear impressions of surface sculpture, one also having an internal mold counterpart; one internal mold with traces of exterior sculpture, diameter 12.1 mm, height 8.2 mm, with 5.5 whorls; four specimens with considerable shell remaining and very good preservation of protoconch sculpture (Fig. 20), diameter 4.6–9.7 mm, with 3.25–4 whorls. USGS 20014, two specimens—one a basal external mold 10.4 mm in diameter of an umbilicate shell with somewhat tumid base, low, forwardly concave, radial ribbing, and minor spiral rugosity; the other a shell 3.5 mm in diameter, in matrix, no sculpture preserved. USGS 20016, one external mold with internal mold counterpart, 9 mm in diameter, the matrix coarse but preserving radial riblets on the protoconch. USGS 20017, five specimens—one external and four internal molds, the largest 13.5 mm in diameter; three of the internal molds with some original shell remaining, showing angulate periphery, retractive axial ribbing, and fine, incised spiral lines on the shoulder; one with strongly ribbed protoconch well preserved.

REMARKS.—The type-lot consists of moderately well preserved to very well preserved origi-

nal shells and internal molds with matrix of cream-colored to yellowish gray, limy, tuffaceous siltstone. The paratypes range from 2.2 mm in diameter with 2.2 whorls to 11.4 mm in diameter with 5.3 whorls. Specimens of fewer than 4 whorls are acutely carinate, with the carina above the middle of the whorl, set off in some instances by faintly impressed grooves above and below. Some adult shells show minor spiral ribbing in addition to incised spiral striae on the last 0.25–0.5 whorl.

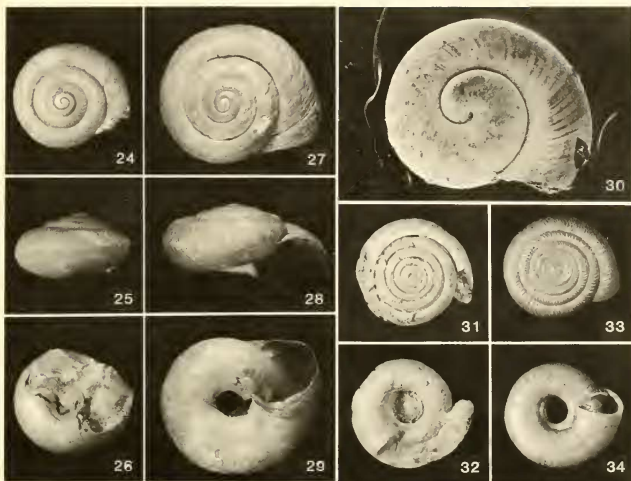
This is the most ubiquitous species in the Dunbar Creek Formation, occurring at five out of the seven localities that yielded land snails.

Radiocentrum taylori resembles the Holocene *R. chircahuanum* (Pilsbry, 1905), another low-trochoid species with strong, irregular ribbing and an angulate to carinate periphery. The strongest resemblance is to the subspecies *R. c. obsoletum* (Pilsbry and Ferriss, 1910) (Fig. 21–23), in which the incised spiral sculpture is weak, the ribbing coarse and blunt, and the peripheral keel not especially prominent. The periphery of *R. taylori* is less carinate, most often acutely angular in subadult to adult shells, less commonly with spiral grooves setting off a peripheral keel. *Radiocentrum c. obsoletum* attains larger size, up to 15 mm diameter; *R. c. chircahuanum*, at about 11 mm, is similar in size to *R. taylori*.

Radiocentrum taylori differs from *R. laevidomus*, next described, from the Milligan Creek Formation, in its coarser sculpture and higher-spined, trochoid shape. *Radiocentrum laevidomus* lacks the spiral sculpture of *R. taylori*; its protoconch has fine, simple ribs instead of the heavy, overhanging ribs of *R. taylori*.

Radiocentrum (?) anguliferum (Whiteaves, 1885) from the upper Cretaceous of Alberta differs in its very low spire and nearly involute mode of coiling. *Radiocentrum thurstoni* (Russell, 1926) from the Paleocene of Alberta has a subangular to rounded periphery and narrow umbilicus. It is also larger than any *R. taylori* specimens yet seen.

Radiocentrum hendersoni (Russell, 1938) from the Oligocene of Colorado is similar to *R. taylori* in its low-trochoid shape, prominent radial ribbing, and shouldered whorls. At 7.8 mm in diameter, with 4.5 whorls, the holotype of *R. hendersoni* (Fig. 13–15) may be immature. However, the last whorl descends below the peripheral angle, the shouldering of the whorl is intensified, and the inner lip expands toward the umbilicus,



FIGURES 24-34: Figures 24-26, 30. *Radiocentrum laavidomus*, new species. Figures 24-26, holotype, USNM 377387; diameter 10.1 mm. Figure 30. Paratype (hatchling young), USNM 377388; diameter 1.6 mm. Figures 27-29. *Radiocentrum hachetatum* (Pilsbry), CAS 046509; diameter 14.2 mm; Holocene, summit of Hacheta Grande Mountain, Hidalgo County, New Mexico. Figures 31, 32. *Polygyrella* sp., cf. *P. polygyrella* (Bland and Cooper), USNM 377391; diameter 10.1 mm. Figures 33, 34. *Polygyrella polygyrella* (Bland and Cooper), CAS 046510; diameter 10.1 mm; Holocene, 2.4 km south of Selway Falls, Idaho County, Idaho. All specimens coated for photographing.

as in mature specimens of other oreohelicids. A 4.5-whorled paratype of *R. taylori* (Fig. 19) is 8.2 mm in diameter, lacks the incised spirals that decussate the ribs in *R. hendersoni*, and has a much less profoundly impressed suture.

I take pleasure in naming this species for Dwight W. Taylor, expert on freshwater Mollusca of western North America and author of the first reports on its occurrence.

Radiocentrum laavidomus new species

(Figures 24-26, 30)

Oreohelix n. sp., D. W. Taylor in Robinson 1963:68, table 4 (in part).—Taylor 1975:206.

DIAGNOSIS.—A small, lenticular *Radiocentrum* of about 5 whorls; periphery angulate above middle of whorl; protoconch sculpture of fine,

low-standing, smooth radial riblets separated by wider interspaces; neanic sculpture of low, irregular radial striae; no spiral sculpture present.

DESCRIPTION.—Shell lenticular, apical angle 133°. Whorls about 5, enlarging rapidly; whorls of spire moderately convex, suture impressed. Body whorl expanding at about same rate as spire whorls, not descending behind aperture; periphery angulate above middle of whorl, becoming gently rounded on last 0.25 turn of 5-whorled specimen. Base rather deep, moderately inflated; umbilicus conical, its diameter contained three to four times in diameter of shell, with a hint of carination at its rim. Aperture simple, without thickening. Protoconch of 1.75 whorls, nuclear tip smooth, followed by smooth, regular, forwardly convex radial ribs separated by interspaces of greater width, increasing in strength

and distance to end of protoconch; ribs extending from suture to shoulder, weak to obsolete over periphery, then reappearing as a series of fine riblets spiraling inward around umbilicus of juvenile shells. Neanic whorls sculptured with low, irregular, forwardly convex radial striae. Striae strongest below suture, sometimes interrupted or deflected backward at peripheral angulation. Dimensions of holotype: diameter 10.1 mm, height 5.6 mm, whorls 4.6; of largest well-preserved paratype (USNM 377389): diameter 10.3 mm, height 6.5 mm, whorls 5.3.

TYPE-MATERIAL.—Holotype: USNM 377387, from U.S. Geological Survey Cenozoic Locality 20007, Montana: Gallatin County: NW¼ SW¼ sec. 36, T 1 N, R 1 W, Three Forks Quadrangle (1950) 1:62,500; altitude 4,260 ft (1,300 m). Milligan Creek Formation, Eocene (?). Measured paratype: USNM 377389; figured paratype: USNM 377388; and 24 additional paratypes, USNM 377390, all from same locality as holotype.

REMARKS.—The type-lot consists of well-preserved original shells with matrix of solid to friable tan to cream-colored limestone. Color pattern is preserved on some specimens. The paratypes range from 1.5–5+ whorls. Sixteen of these are little more than hatchling young of 1.5–2.0 whorls (Fig. 30). The presence of such small juveniles free in the matrix indicates that the species was probably oviparous like modern *Radiocentrum*. In *Oreohelix*, the embryos are retained *in utero* to a stage of 2 whorls or more.

The spire of the holotype and of the largest well-preserved paratype are mottled with orange-brown blotches at intervals of 0.1–0.5 whorl. The blotches extend either inward or outward from the suture, in a few cases crossing an entire whorl, but do not pass from one whorl to the next. They are probably remnants of an original color pattern. Many specimens of the Holocene species *R. hachetanum* (Pilsbry, 1915) and *R. chiricahuatum* (Pilsbry, 1905) show similar mottling.

The species most similar to *R. laevidomus* in general shape and sculpture is the Holocene *R. hachetanum* (Fig. 27–29). The fine spiral lines in the intervals between protoconch ribs on *R. hachetanum* are not visible on *R. laevidomus*.

This species differs from *R. taylori* of the Dunbar Creek Formation in its finer, more delicate sculpture on both protoconch and neanic whorls, its lower spire, and lenticular rather than trochoid shape. The radial ribs on the protoconch of *R. taylori* are elevated, prominent, somewhat overhanging on the abapertural side, and nearly

as wide as their interspaces. Those of *R. laevidomus* are low-standing, evenly rounded, and distinctly narrower than their interspaces. Ribs on the very young paratypes, which could not have been subjected to much wear, have the same character (Fig. 30). *Radiocentrum laevidomus* shows no spiral sculpture like that present on *R. taylori*. Approximately the same characters differentiate *R. laevidomus* from *R. chiricahuatum*, which is very similar to *R. taylori* as noted above.

Radiocentrum(?) anguliferum (Whiteaves, 1885) from the upper Cretaceous of Alberta differs from *R. laevidomus* in its strongly angular periphery and nearly involute mode of coiling. *Radiocentrum hendersoni* (Russell, 1938) from the Oligocene of Colorado differs in its higher-spired, trochoid shell, strong radial ribbing, and very deeply impressed suture. *Radiocentrum thurstoni* (Russell, 1926) from the Paleocene of Alberta is another trochoid species, with a higher, more conical spire. According to Tozer (1956) the embryonic whorls of *Oreohelix obtusata* (Whiteaves, 1885), upper Cretaceous of Alberta, are apparently smooth, which would rule out assignment to *Radiocentrum*.

The name proposed combines the Latin *laevis*, smooth, with *domus*, house, in reference to the relatively faint sculpture of the shell.

Family AMMONITELLIDAE

Polygyrella Binney, 1863

TYPE-SPECIES.—*Helix polygyrella* Bland and Cooper, 1861, by monotypy.

DIAGNOSIS.—“The shell is widely umbilicate, discoidal with convex to nearly flat spire of narrow, closely coiled costulate whorls; base smooth, translucent. Aperture lunate-triangular, the unexpanded peristome somewhat thickened within, the ends connected by an erect, triangular parietal tooth. Within the last whorl there are one or two radial series of three teeth each. Jaw with flat plaits and fine vertical striae. Soft anatomy . . . about as in *Ammonitella*” (Pilsbry 1939: 555–556).

REMARKS.—*Polygyrella* is represented in the Holocene by one species, *Polygyrella polygyrella* (Bland and Cooper, 1861), with a range of northern Idaho, adjacent Montana, southeastern Washington, and northeastern Oregon. *Polygyrella* from the John Day Formation (late Oli-

gocene or early Miocene) of central Oregon are referred to the same species (Hanna 1920).

Taylor (1975) assigned specimens from the Eocene Kingsbury Conglomerate Member of the "Wasatch" Formation in the Powder River Basin, Wyoming, to *Polygyrella*. He further suggested that *Planorbis amplexus* Meek and Hayden, 1857 (upper Cretaceous, Judith River Formation, Montana), and *Anchistoma parvulum* Whiteaves, 1885 (upper Cretaceous, St. Mary River Formation, Alberta), are both species of *Polygyrella*. Based on its pattern of coiling, basal configuration, and parietal barrier, *Polygyra venerabilis* Russell, 1937, from the upper Cretaceous Belly River Formation, Alberta, seems to be another. Indeterminate species of *Polygyrella* are reported from upper Eocene strata in Glacier National Park, Montana (D. W. Taylor in Ross 1959), and (questionably) from an unnamed conglomeratic sequence of presumed early Tertiary age on Little Granite Creek, Hoback Basin, northwestern Wyoming (Taylor 1975).

Polygyrella* sp., cf. *P. polygyrella
(Bland and Cooper, 1861)

(Figures 31, 32)

Polygyrella, D. W. Taylor in Robinson 1963:68, table 4.—Taylor 1975:208.

DESCRIPTION.—Shell subdiscoidal with broad umbilicus contained approximately three times in diameter. Spire flat to low-convex, suture lightly impressed. Whorls tightly coiled, sometimes with closely spaced, forwardly convex radial grooves extending outward from suture, not reaching shoulder of whorl. Body whorl with up to four shallow transverse constrictions. Last whorl not markedly descending except immediately behind aperture. Aperture oblique, peristome thickened and slightly expanded outward.

REFERRED MATERIAL.—Climbing Arrow Formation: USGS 20008, 5 specimens. USGS 20009, 14 specimens.

REMARKS.—The material from the Climbing Arrow Formation consists of internal molds (and some thoroughly recrystallized shells) shaped much like the modern *Polygyrella polygyrella* (Fig. 33, 34), with the subdiscoidal shape, flat to low-domed spire, tightly coiled whorls, and broad, circular umbilicus of that species. The fossils are composed in part of translucent, colorless to honey-colored, coarsely crystalline calcite, either replacing the shell or conforming to its interior,

and in part of pinkish tan, finely crystalline calcite probably representing a limy mud that partially filled the shells upon burial.

The peristome is moderately thickened in several specimens from locality USGS 20009; these are probably mature individuals. In them, the aperture slants at a 45° angle to the axis of coiling, the same as in *P. polygyrella*. Juvenile specimens of 4 whorls or less are planorboid, with much of the protoconch visible in the umbilicus.

Two distinctive shell features of *P. polygyrella* are not detectable: an erect parietal tooth and a radial series of barriers inside the last whorl. Careful preparation around the aperture of two specimens with mature, expanded peristomes revealed no parietal tooth. If completely recrystallized, such a tooth might not be distinguishable from other calcite filling the whorl; the same may be true for the series of barriers that would be expected about one-half whorl back of the aperture. One specimen from locality USGS 20009 shows radial grooves outboard of the suture on what is apparently the fourth whorl, corresponding to interspaces between radial costae on the spire of *P. polygyrella*.

The six largest specimens measure

Locality	Diameter	No. of whorls
USGS 20008	10.2 mm	7.1
	9.1	6.8
	8.6	6.7
USGS 20009	9.0	6.2*
	9.0	6.2*
	8.0	5.9

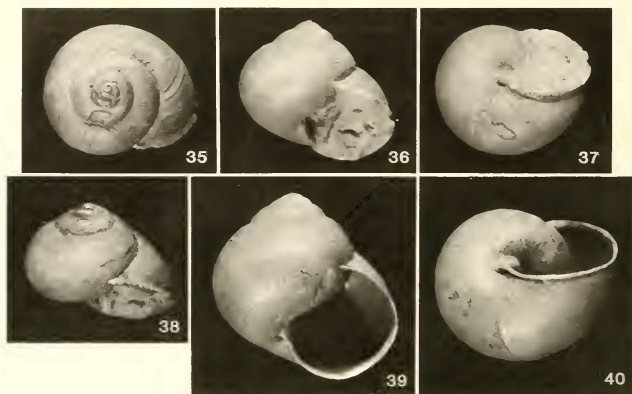
Asterisks denote specimens with mature expanded peristome.

Polygyrella parvula (Whiteaves, 1885) differs from *P. polygyrella* and the present specimens in its conoidal spire, sharply descending body whorl, and single slanting internal barrier. As illustrated (Meek 1876, pl. 42, fig. 16a–16c; Shimer and Shrock 1944, pl. 213, fig. 14, 15), *P. amplexa* (Meek and Hayden, 1857) is flat-spined or nearly so, with an umbilicus that is more conical than the steep-sided, pitlike umbilicus of *P. sp.*, cf. *P. polygyrella*. No information is available on the presence or configuration of internal barriers in *P. amplexa*, and the aperture is unknown.

Family HELMINTHOGLYPTIDAE

***Helminthoglypta* Ancey, 1887**

TYPE-SPECIES.—*Helix tudiculata* Binney, 1843, by original designation.



FIGURES 35-40: Figures 35-38. *Helminthoglypta bozemanensis*, new species, holotype, USNM 377392; diameter 16.6 mm. Figure 38, oblique view showing color banding. Figures 39, 40. *Helminthoglypta californiensis* (Lea), CAS 046511; diameter 19.3 mm; Holocene, Pacific Beach, north of Monterey, Monterey County, California. All specimens except Figure 38 coated for photographing.

DIAGNOSIS.—“Helices of moderate or large size, the shell globose or depressed with conic or low spire and open or covered umbilicus; periphery rounded at all stages of growth. Embryonic shell of $1\frac{1}{2}$ to $1\frac{3}{4}$ whorls; after the smooth tip and a few radial wrinkles it has sculpture of close, microscopic, waved, radial wrinkles, over which there are papillae in forwardly descending trends (often indistinct or practically absent). Adult sculpture of simple growth lines or with spiral engraved lines, malleation, papillae or granulation also. A dark band revolves above the periphery (sometimes absent). Peristome narrow, expanded outwardly, usually reflected at base, dilated at columellar insertion” (Pilsbry 1939: 63).

REMARKS.—The genus *Helminthoglypta* today is distributed from southeastern Oregon, through California west of the Cascade Range and the crest of the Sierra Nevada, into northern Baja California, Mexico. About 55 species are recognized. At the northern end of the range of the genus, *Helminthoglypta mailliardi* Pilsbry, 1927,

and *H. hertleini* Hanna and Smith, 1937, inhabit low elevations in the Klamath Mountains. At the southern end, *H. tudiculata* (Binney, 1843) and *H. traskii* (Newcomb, 1861) extend along the coast to the vicinity of San Antonio del Mar, Colinet, and *H. reederi* Miller, 1981, occurs in the Sierra San Pedro Mártir (Miller 1981b). One species, *Helminthoglypta alfi* Taylor, 1954, occurs in the Barstow Formation, upper Miocene of the Mojave Desert, California; it is similar to Recent Mojave Desert species. An undescribed species occurs in strata of probable Pliocene age in the Tehachapi Mountains, California (Roth, unpublished data). The Eocene species *Helminthoglypta obtusa* Anderson and Hanna, 1925, from the Tejon Formation, and *H. (?) stocki* Hanna, 1924, from the Sespe Formation, California, are probably incorrectly assigned to *Helminthoglypta*, but more material will have to be studied before a better allocation can be made. A land snail tentatively identified as *Helminthoglypta* is present in the Wiggins Formation (Oligocene), Wind River Basin, Wyoming (Taylor 1975).

***Helminthoglypta bozemanensis* new species**

(Figures 35–38)

Helminthoglyptidae n. gen., D. W. Taylor in Robinson 1963: 68, table 4.

Hemitrochus? Taylor 1975:208, 209.

DIAGNOSIS.—A small, globose-conic *Helminthoglypta* of about five whorls; body whorl weakly constricted behind reflected outer lip; umbilicus narrow, obliquely entering; sculpture of blunt incremental rugae and granulose vermiculation sometimes resolving into radial rows of granules; narrow dark peripheral band present, bordered above and below by wider light zones; less distinct dark zones on shoulder and just below suture.

DESCRIPTION.—Shell globose-conic, wider than tall, apical angle 107°. Whorls about 5, convex, rapidly expanding; suture impressed. Body whorl tumid, strongly descending for last 0.25 turn and more strongly for last 0.1 turn, weakly constricted behind outer lip. Aperture subcircular; parietal wall shallowly sigmoid, with thin wash of callus; peristome reflected and narrowly expanded, smooth at edge, more strongly reflected and thickened in umbilical region. Base well-rounded; umbilicus very narrow, scarcely perforate, obliquely entering behind inner lip. Protoconch smooth, probably consisting of about 1.8 whorls. Neanic whorls sculptured with (a) moderately strong, blunt, oblique incremental rugae, most irregularly spaced but some rhythmically spaced at intervals of about 1.0 mm, strongest on whorl shoulder but continuing over base, and (b) low granulose vermiculation, strongest between rugae and generally trending parallel to them. Vermiculation weaker on base and behind outer lip, where it generally appears as radial rows of blunt, axially elongate granules. Body whorl with narrow (0.8 mm-wide) brown supraproperipheral band, bordered above and below by slightly wider (1.2 mm) zones lighter than ground color of shell, and less distinct dark zones on midshoulder and just below suture. Dimensions of holotype: diameter (exclusive of expanded lip) 16.6 mm, height 13.3 mm, whorls 4.8; dimensions of paratype: diameter (slightly distorted) 15.4 mm, height 13.9 mm, whorls 5.2.

TYPE-MATERIAL.—Holotype: USNM 377392, from U.S. Geological Survey Cenozoic locality 20011, Montana: Broadwater County: SE¼ NW¼ sec. 6, T 2 N, R 2 E, Three Forks Quadrangle (1950) 1:62,500; altitude 4,360 ft (1,330 m). Dun-

bar Creek Formation, Eocene or Oligocene. Paratype: USNM 377393, from same locality as holotype.

REFERRED MATERIAL.—Four additional specimens from the USGS collection are referable, with differing degrees of confidence, to *Helminthoglypta* and *H. bozemanensis*. Climbing Arrow Formation: USGS 20009, one specimen, a fragment of smooth apical whorls and partial spire, 5 mm in greatest diameter, probably assignable to *Helminthoglypta*. Dunbar Creek Formation: USGS 20015, two specimens, internal molds, (1) diameter 7.4 mm, height 5.6 mm, whorls 3.4, and (2) diameter 9.8 mm, height 8.9 mm, whorls 3.8; small amount of shell material remaining on latter shows spaced incremental rugae oriented as on holotype, surface detail not preserved; raised line on internal mold in position of supraproperipheral band: = *Helminthoglypta* sp., cf. *H. bozemanensis*. USGS 20016, one specimen, internal mold, diameter 13.0 mm, height 10.5 mm, whorls 4.1. = *Helminthoglypta* sp., cf. *H. bozemanensis*.

REMARKS.—The holotype (Fig. 35–38) is a very well preserved specimen with almost all the original shell remaining and clear indication of the former position of color bands. The paratype is an internal mold with little shell remaining, the spire somewhat collapsed into the body whorl.

This species is assigned to *Helminthoglypta* because of the distinct supraproperipheral band, shape, sculpture, and reflected peristome. There are particularly strong similarities to the Recent *Helminthoglypta californiensis* (Lea, 1838) (Fig. 39, 40) of the central California coast. The weak constriction of the body whorl immediately behind the evenly expanded outer lip, and the extent to which the last quarter-whorl descends are identical in both species. The fine sculpture of *H. californiensis* consists of rows of axially elongated granules paralleling the incremental lines. In many specimens, the granules correspond rather loosely from one row to the next. In other specimens, and in other members of the "*Helminthoglypta nickliniana* series" (Pilsbry 1939), to which *H. californiensis* belongs, the granules may line up quite precisely in diagonal rows, producing a distinctive clothlike pattern. In *H. bozemanensis*, where the granulose vermiculation most clearly resolves into rows of discrete granules (mainly on the base and behind the outer lip), the sculpture strongly resembles that of *H. californiensis*.

Taylor (1975) ruled out assignment to *Helminthoglypta* because of the multiple color bands, not otherwise known in the genus, and questionably referred these specimens to *Hemitrochus* Swainson, 1840 (type-species, *Hemitrochus hoemastomus* Swainson, 1840 [= *Helix varians* Menke, 1829], by monotypy). *Hemitrochus* con-

sists of about 25 Recent species distributed in southern Florida and the Antilles (Pilsbry 1889-90, 1893-95; Turner 1958).

The dim bands at the shoulder and suture of *Helminthoglypta bozemanensis* are located where the margins of the dark shoulder zone occur in modern *Helminthoglypta*. Several instances exist, in Helminthoglyptidae and other families, of vacant-centered bands as a polymorphism of banded shells (Roth 1981a, *Monadenia*; Roth and Bogan 1984, *Liguus*). The upper and lower shell bands in the helminthoglyptid genus *Humboldtiana* Ihering, 1892, for which Pilsbry (1939) could not suggest a homology, may have originated in this way, as the emphasized edges of two now-vanished broad zones. The central band in *Humboldtiana* is probably homologous with the supraperipheral band of most other Helminthoglyptidae. The upper and lower bands bracket the central band about as evenly as the dark zones top and bottom on a *Helminthoglypta* shell. The strengths of the upper and the lower band are strongly correlated, but apparently independent of the strength of the central band, suggesting a different derivation.

Because of the apparent ease of the transformation from solid to vacant-centered band, I do not think that the banding pattern of *H. bozemanensis* precludes assignment to *Helminthoglypta*. Other similarities to *Hemitrochus* do exist, however. They include the smooth protoconch, obliquely entering umbilicus, and spaced incremental rugae. In no Recent species of *Hemitrochus* do the whorls enlarge as rapidly; in globose-conic species, the spire makes up more of the shell. The base is typically shorter, tending to be flattish rather than tumid, and the strongest color band is usually at or below the periphery. The extent to which the lip turns out at maturity varies with the species, but often there is additional thickening inside the edge of the aperture, which is not present in *Helminthoglypta bozemanensis*.

Taylor (1975) also reported shells that he assigned to *Hemitrochus*? from the White River Formation (Oligocene), Beaver Divide area, central Wyoming. La Rocque (1960) noted the similarity of "*Helix*" *riparia* White, 1876, from the Flagstaff Formation, Paleocene and Eocene of Utah, to *Hemitrochus* but declined to make a firm generic assignment for the species.

Of the other helminthoglyptid genera that might be compared, *Leptarionta* Fischer and

Crosse, 1872, has a glossy or silky shell with growth lines hardly evident in relief. *Xerarionta* Pilsbry, 1913, and *Plesarionta* Pilsbry, 1939, both have incised spiral sculpture that is not present in *Helminthoglypta bozemanensis*. *Humboldtiana* has compound sculpture consisting of incremental rugae and blunt granulation (sometimes, as in *H. palmeri* Clench and Rehder, 1930, partly fusing into an irregular vermiculation). The possible homology of *Humboldtiana*'s three bands with the pattern of *Helminthoglypta bozemanensis* has already been mentioned. However, no Recent *Humboldtiana* has the globose-conic shape of *H. bozemanensis*; in *Humboldtiana* the protoconch is finely pustulose, its juncture with the teleoconch well marked; the outer lip is barely reflected, and there is no constriction behind the aperture. *Lysinoe* Adams and Adams, 1855, has, in addition to growth rugae, regularly spaced, discrete papillae (corresponding to the bases of periostracal bristles) in diagonal series. Nothing similar is present in *H. bozemanensis*.

Because of the supraperipheral band (a form of disruptive coloration), it is assumed that the periostracum of *H. bozemanensis* was transparent, although vestigial banding occurs under an opaque periostracum in *Monadenia* (Roth 1981b).

FAUNAL COMPOSITION AND PALEOECOLOGY

MILLIGAN CREEK FORMATION.—The faunule from the Milligan Creek Formation consists of two species of *Gastrocopta* (*Albinula*) and one species of *Radiocentrum*. The only species that may have a stratigraphic record outside the formation is *G. montana*, which is provisionally recognized in the Dunbar Creek Formation.

The two *Gastrocopta* species seem to be most closely related to *Gastrocopta* (*Albinula*) *contracta*, which I regard as a plausible ecological analog. *Gastrocopta contracta* ranges over much of eastern North America, as far west as South Dakota, Oklahoma, and western Texas (Pilsbry 1948; Cheatum and Fullington 1973). It extends farther west in Mexico, reaching southern Sonora (Arroyo San Rafael, San Bernardo) and northern Sinaloa (San Blas) (Pilsbry 1953). In the United States its western limit coincides approximately with the 16-inch [41-cm] normal annual isohyet (U.S. Department of Commerce 1968). *Gastrocopta contracta* does not occur in western Montana but *Albinula* in the broad sense is present in the form of *G. holzingeri*.

The modern habitat of *Gastrocopta contracta* is on shaded slopes along watercourses, under dead wood, leafmold, and grass (Franzen and Leonard 1947, referring to Kansas). It is recorded from dense vegetation in mixed mesophytic forest in Kentucky (Branson and Batch 1970). No ecological notes on its Mexican occurrences are available. Other species of *Albinula* occur on wooded slopes, either near or away from streams, under dead wood, bark, stones, and in moist grass around seepages (Franzen and Leonard 1947; Taylor 1960).

Radiocentrum does not now range north of Santa Catalina Island, California, southern Arizona and New Mexico, and trans-Pecos Texas. Its habitat is generally in mountainous terrain, among cliffs and rockslides, usually where vegetation is sparse. It is not an inhabitant of forests. At least two species are reported to be restricted to limestone (Pilsbry 1939), but others occur on shale or among lava rockslides (Pilsbry 1939; Miller 1973a). On Santa Catalina Island, *R. avalonense* (Pilsbry, 1905) occurs on steep slopes of talus where the country rock is granitic, around the roots of black sage (*Salvia mellifera*) shrubs (Hochberg et al., in press). Modern disjunctions within the range of *Radiocentrum* are closely linked to zones of extreme aridity—the Sonoran and Chihuahuan deserts (Hochberg et al., in press). The southern Arizona and New Mexico occurrences are in isolated areas receiving at least 41 cm annual precipitation, at least half of it in the summer months (U.S. Dept. Commerce 1968).

Radiocentrum and *G. contracta* are not known to be sympatric anywhere at present; the two groups come closest in western Texas—*Radiocentrum* in El Paso County (Metcalf and Johnson 1971) and *G. contracta* in Culberson, Jeff Davis, and Presidio counties (Cheatum and Fullington 1973). However, the range of *Radiocentrum* is apparently contracting, with several peripheral occurrences known only from empty shells, and there may have been limited sympatry within the recent past in either the southwestern United States or northern Mexico.

The *G. contracta*-like species in the Milligan Creek Formation imply somewhat more mesic conditions (possibly at the microhabitat level) than does *Radiocentrum*. Robinson (1961, 1963) concluded that the limestone and other fine-grained rocks of the Milligan Creek Formation were deposited in a perennial lake lying in moun-

tainous terrain. The habitat of the *Gastrocopta* species may have been in leafmold along wooded watercourses feeding the lake. *Radiocentrum laevidomus* may have lived in more sparsely vegetated habitats nearby. Its source area was probably not remote, however, as it is the numerically dominant species in the USGS sample. The indicated climate is warm-temperate to subtropical. A minimum of 40 cm annual precipitation is suggested, much of it in the summer months. The land snails do not indicate a frost-free climate; within the southern Arizona–New Mexico range of *Radiocentrum* there is a period of generally less than 200 days between the last freeze of spring and the first freeze of autumn. Over much of the eastern range of *Gastrocopta contracta* the frost-free period is even shorter (U.S. Dept. Commerce 1968).

CLIMBING ARROW FORMATION.—The faunule from the Climbing Arrow Formation consists of *Gastrocopta* (*Albinula*) *sagittaria*, *Polygyrella* sp., cf. *P. polygyrella*, and a fragment of apical whorls and incomplete spire probably assignable to *Helminthoglypta*. The *Gastrocopta* is not known to occur outside the formation. The present material does not allow a determination whether the *Helminthoglypta*(?) is the same as *H. bozemanensis* of the Dunbar Creek Formation. The *Polygyrella* species, although not adequately preserved, does not seem to differ in any significant way from *Polygyrella polygyrella*, which ranges from late Oligocene or early Miocene (Hanna 1920) to Holocene.

As already noted, *Gastrocopta* (*Albinula*) is basically an eastern group at present, with one species entering western Montana. The only modern species of *Polygyrella*, *P. polygyrella*, ranges through northern Idaho and adjacent parts of Montana, southeastern Washington, and northeastern Oregon (Pilsbry 1939; Smith 1943). There are no records from as far east as the Three Forks Quadrangle. The original locality for *P. polygyrella* was on the eastern slope of the Coeur d'Alene Mountains, in moss and decaying wood in damp spruce forest. At Cataldo, Idaho, it was found in schist rockslides near the base of east-facing slopes near the Coeur d'Alene River; on lava rock, as at Stites, Idaho, it buries itself in the black, coarsely granular soil beneath the rockslides (Pilsbry 1939). Smith (1943) found it in lava rockslides and reported it to be common at lower elevations in the Clearwater Mountains of Idaho. The main part of its range is in a moun-

tainous region that receives ~50–75 cm annual precipitation; just eastward in the rain shadow of the Continental Divide the precipitation falls off sharply to half or a third of this total (U.S. Dept. Commerce 1968). A large proportion of this precipitation falls as rain in the months of April, May, and June.

The indicated environment is temperate, cooler and wetter than that of the Milligan Creek Formation. Both *Polygyrella* and the *Gastrocopta* are suggestive of wooded conditions, perhaps mature forest with plenty of wood on the ground. Shaded rockslides adjoining wooded streambanks are another possibility. The fine-grained, bentonitic sediments of the Climbing Arrow Formation suggest low relief in the immediate area, so perhaps humid forest is the more plausible environment. It is compatible with the flood plain deposition inferred by Robinson (1963). The Three Forks Basin may have drained eastward (Robinson 1961), but it was undoubtedly not in a Cordilleran rain shadow as at the present time.

The ecological significance of *Helminthoglypta* is discussed more fully below under the Dunbar Creek Formation. It is consistent with an equable, mesic climate, although *Helminthoglypta* and *Polygyrella* are strictly allopatric at present.

The presence of the tropical freshwater snail *Biomphalaria pseudammonius* contradicts the temperate climatic inferences based on the land snails. According to Taylor (1985), *B. pseudammonius* is doubtfully distinct from the living *B. glabrata*, which has an optimum reproductive temperature of 25°C and fails to reproduce at 20°C. The *Biomphalaria* is from a different locality (USGS 20010) than the land snails, in an adjoining section, 50–55 m topographically lower. It seems unlikely that there was enough local relief to throw temperate (i.e., as from higher-altitude) and tropical faunal elements into juxtaposition.

Konizski (1961) described the paleoecology and inferred climate of a biota (including *Biomphalaria* cf. *B. pseudammonius*) from the Douglas Creek Basin, Montana, approximately 150 km northwest of the Three Forks Basin. The vertebrate fauna is similar to the Pipestone Springs fossil assemblage, correlative with the upper part of the Climbing Arrow Formation but probably somewhat younger than the beds yielding the land gastropods. Plant remains, determined by Axelrod, indicate that the climate was temperate "but whether it was warm temperate . . . is not

now known. Rainfall was distributed in summer and winter and was not less than 30 to 35 inches. Winters appear to have been comparatively mild, but the frequency of frost or snow cannot be determined from the material at hand" (D. I. Axelrod in Konizski 1961:1639). Konizski concluded that the climate was temperate and probably varied seasonally; winters were mild compared to the present. Plant associations were stratified by altitude. The vertebrate assemblage suggests montane woodland rather than a savannah or open plains environment. The sedimentology indicates a basin profile of low relief with erosion a function of chemical as well as mechanical weathering.

Robinson (1963) suggested that part of the Climbing Arrow Formation may have been deposited contemporaneously with the Milligan Creek Formation, but the environments inferred from *Polygyrella*, on the one hand, and *Radiocentrum* on the other, are so distinct that facies difference seems an inadequate explanation.

Taylor (1975:204) remarked that the molluscan collections from the Climbing Arrow Formation are of special interest "because they provide a stratigraphic tie with late Eocene and early Oligocene fossil vertebrates in this area." It is unfortunate therefore that the *Polygyrella* may be a stratigraphically long-ranging species and that the helminthoglyptid is not represented by better material. *Gastrocopta sagittaria*, with its distinctive, ovate-conic shape, may prove to have biostratigraphic utility.

DUNBAR CREEK FORMATION.—The faunule from the Dunbar Creek Formation consists of two species of *Gastrocopta*, two of *Pupoides* (*Ischnopupoides*), *Radiocentrum taylori*, and *Helminthoglypta bozemanensis*. *Gastrocopta cordillerae*, *Pupoides tephrodes*, and *Radiocentrum taylori* are known only from this formation. *Gastrocopta* sp. cf. *G. montana* may be the same species present in the Milligan Creek Formation. *Helminthoglypta bozemanensis* is questionably present in the Climbing Arrow Formation.

The phylogenetic affinities of *G. cordillerae* are not known, so it adds no ecological or geographic information to that derivable from *G. sp. cf. G. montana*, discussed above under the Milligan Creek Formation. The same comments made above for *Radiocentrum laevidomus* also apply to *R. taylori*.

Pupoides (*Ischnopupoides*) is indicative of dry conditions. Today, *P. hordaceus* is "a species of

the arid plateaus and foothills [of Colorado, Utah, New Mexico, and Arizona], not found in the humid upper zone of the mountains" (Pilsbry 1948:925). Bequaert and Miller (1973) report it from northern Arizona, living in litter of an arid biotope, under shrubs and low trees, near the top of a steep rocky bluff at an elevation of 5,800 ft [1,800 m]. Both *P. hordaceus* and *P. inornatus* are found only as empty shells in many more localities than they are known living. This suggests that, like *Radiocentrum*, the subgenus is now undergoing local extinction in many parts of its range. The known distribution is not obviously linked to any thermal or precipitation gradient on a regional scale.

Helminthoglypta is now basically a Californian genus, with a few species extending into Oregon and Baja California. It occurs over a wide range of habitats from equable, maritime situations along the coast to highly arid conditions in the Mojave Desert. There is some indication of correlation between shell form and climate. The globose-conic species and subspecies of *Helminthoglypta*—*H. californiensis* (Lea); *H. mailliardi* Pilsbry; *H. fieldi* Pilsbry, 1930; *H. nickliniana awania* (Bartsch, 1919)—are all coastal forms, living in temperate climates with few extremes of temperature. Inland forms on the whole tend to be flatter and more tightly coiled, the extremes being the "Mojave Desert series" (Pilsbry 1939) consisting of small, almost planispiral, widely umbilicate shells with the whorls increasing slowly in size. An exception is *Helminthoglypta berryi* Hanna, 1929, from the foothills of the Sierra Nevada and Tehachapi ranges, an aberrant form that is the most highly fossorial species of the genus. The presence of a strong color pattern in *H. bozemanensis* does not suggest a fossorial mode of life, so that *H. berryi* is probably not as good a modern analog as *H. mailliardi* or *H. californiensis*. To the extent that shell shape in *Helminthoglypta* is correlated with environment, *H. bozemanensis* suggests an equable climate with a mean annual range of temperature of less than 13°C (data from Wolfe 1979). For the coastal species mentioned above the total annual rainfall varies from over 200 cm in the range of *H. mailliardi* to less than 30 cm in the range of *H. fieldi*. The precipitation is concentrated in the winter months, with practically none between May and October (U.S. Dept. Commerce 1968).

Helminthoglypta today is nowhere sympatric

with the other genera; its closest approach to any is on the mainland of Los Angeles County, opposite Santa Catalina Island where *Radiocentrum avalonense* occurs. Without postulating different climatic tolerances for one or more of these genera in the Paleogene, it is hard to reconcile their joint occurrence in the Dunbar Creek Formation. About the only inferences one can draw about the Dunbar Creek environment are that it was probably drier than that of the Climbing Arrow Formation, with sparser vegetation (possibly scrub, savannah, or open woodland), and moderate seasonal variation in temperature and precipitation. Presumed caliche horizons in the Dunbar Creek Formation suggest deposition in a seasonally dry basin or bolson (Robinson 1963) and are compatible with this interpretation.

GENERAL TRENDS.—The land mollusk fauna of the Bozeman Group shows three salient characteristics: (1) the occurrence of several genera well outside their modern ranges; (2) the seemingly paradoxical co-occurrence of genera now widely separated geographically and environmentally; and (3) change through time from sparsely vegetated to forested terrain and back again.

Tropical to subtropical climates extended to high latitudes during the early Tertiary (Durham 1950; Savin et al. 1975; Savin 1977; Wolfe 1978; Lillegraven 1979). Not all taxa in the Bozeman Group, however, show the simple southward shift of range that one would expect if temperature tolerance were the sole determining factor. *Polygyrella* still occupies the same general region. *Helminthoglypta* now lives along the Pacific Coast, extending from cool-mesic to warm and arid environments. *Radiocentrum* has undergone a southward shift to the American southwest, where it lives in rocky habitats but is apparently excluded from regions of extreme aridity. *Gastrocopta* is absent from the west coast but widely distributed in the eastern states; the subgenus *Albinula* approaches but does not overlap the range of *Radiocentrum*.

The present range limitations of *Radiocentrum* may involve interactions between genera as well as simple environmental tolerances. The ovoviviparous *Oreohelix* is now the dominant genus of large land snails throughout much of the Cretaceous-early Tertiary range of *Radiocentrum* (Bequaert and Miller 1973, fig. 4). Except for some work on the agonistic behavior of slugs (Rollo and Wellington 1977, 1979), little

is known about molluscan interactions that could lead to competitive exclusion. However, it is possible that in a climatic context of increasing summer drought and seasonal temperature variation the ovoviviparous mode might have permitted larger and more stable populations of *Oreohelix* to exist, which then outcompeted *Radiocentrum* for limiting resources such as shelter sites.

A mixture of diverse present-day biogeographic elements also existed in the British Isles during the Paleogene, among plants and insects as well as land mollusks (Preece 1982 and references cited therein). Daley (1972) argued that those apparently paradoxical associations represent a climate that has no close modern analog: seasonal but frostless, with high rainfall, and temperatures elevated but not as high as those of tropical rain forest areas today.

Table 2 lists land mollusks from western North America (the western Great Plains to the Pacific Coast) that have a Tertiary or late Cretaceous fossil record outside the Holocene ranges of their families or genera. Many fossil land snails are difficult to assign taxonomically (there is even debate over whether certain species are prosobranchs or pulmonates), hence a number of the generic assignments are provisional. Major differences of interpretation are annotated. It is beyond the scope of this paper to resolve some of the more difficult taxonomic problems involving these species, but in most cases the biogeographic and paleoenvironmental conclusions are not radically affected. Taxa that are wholly problematic because of inadequate type material (e.g., "*Eucalodium*" *eophilum* Cockerell, 1915) or without any convincing modern analogs (Grangerellidae) are excluded.

From this table it is apparent that families and genera now distributed in many other parts of the world were present in western North America in the late Cretaceous and early Tertiary. The largest block of taxa now exists in the American tropics, but almost as many groups now occur in tropical regions of Africa, Asia, and the Pacific Islands as well as in a Pacific coastal belt extending from Alaska to northern Baja California. Another large group now lives in warm-temperate to subtropical parts of the southern United States and Mexico. Others show minor displacement within the western interior. None of the taxa are now restricted to far northern America or Eurasia; those are young molluscan faunas, derived as species from middle latitudes colonized deglaciated regions in Pleistocene to Ho-

locene time. Lower-latitude Tertiary fossil localities (such as those of the lower Miocene of Florida) contain no land snail genera now restricted to higher latitudes.

The main bulk of local extinction seems to have taken place by the end of the Oligocene, but to some extent the evidence is negative: Miocene and Pliocene deposits yielding land mollusks are few. However, Miocene and Pliocene faunas are overwhelmingly composed of genera still extant in the region.

The extinction of many genera of land mollusks over parts of their west North American range may represent the sorting out of formerly sympatric groups into different ecologic/geographic zones. A similar scenario was proposed for the subgenera of *Monadenia* in the Pacific states (Roth 1981a), and a comparable pattern is evidently involved in the origin and development of coniferous forests in the west (Axelrod 1976). It is also possible that if the climatic parameters in the microhabitats of snails were better known, the former association of genera now geographically separated would seem less paradoxical—and the lack of congruence in their modern ranges more attributable to the operations of chance. The answer awaits a closer study of the ecology of living land mollusks.

How much of the environmental change shown by Bozeman Group mollusks is the result of secular climatic change, and how much due to local factors such as tectonism? Radiometric dates associated with faunas of the Chadronian North American Land Mammal "age" range between 37.4 ± 1.2 Ma and 32.3 ± 0.7 Ma (Evernden et al. 1964; Prothero, Dunham, and Farmer 1982). The transition from Uintan to Chadronian faunas occurs within the Climbing Arrow Formation (Robinson 1963). The Eocene-Oligocene boundary, placed at 36.6 Ma (Palmer 1983), probably also occurs within the Climbing Arrow or Dunbar Creek Formation (Fig. 2). (See also correlation by Lillegraven and Tabrum [1983, fig. 2], except that they place the Eocene-Oligocene boundary at 38 Ma.)

Lillegraven summarized the evidence for a late Eocene climatic deterioration, beginning perhaps 5–7 million years before the advent of the Oligocene. He concluded that "the late Eocene and early Oligocene was represented by a world-wide pulse of increased continentality, oceanic cooling, and a significant compression of tropical zones with dilation of temperate conditions. The time was marked by increased rates of extinc-

TABLE 2. TERTIARY AND UPPER CRETACEOUS LAND MOLLUSK TAXA FROM WESTERN NORTH AMERICA (WESTERN GREAT PLAINS TO THE PACIFIC COAST) THAT OCCUR OUTSIDE THE HOLOCENE RANGES OF THEIR FAMILIES OR GENERA

Taxon	Fossil occurrence	Holocene range
Subclass Prosobranchia		
Family Helicinidae		
		Helicinid snails with apertural barriers: Greater Antilles, Mexico, Venezuela, Ecuador, Peru, Bolivia, Brazil (Boss and Jacobson 1975); Laos, Szechuan (Wenz 1938; Bishop 1980)
<i>Eohippitychia eohippina</i> (Cockerell, 1915)	Eocene, Wyoming	
<i>Hendersonia evanstonensis</i> (White, 1878)	Paleocene and Eocene, Wyoming	<i>Hendersonia</i> : E North America (Solem 1979)
<i>H. oregona</i> (Hanna, 1920)	Oligocene or Miocene, Oregon	
<i>Lucidella</i> (?) <i>buttsi</i> (Russell, 1955)	Eocene or Oligocene, British Columbia; Oligocene, Montana	<i>Lucidella</i> : Antilles, Central America (Wenz 1938)
<i>Tozerpina mokowanensis</i> (Tozer, 1956)	Upper Cretaceous, Alberta	Note 1
<i>T. douglasi</i> (Tozer, 1956)	Paleocene, Alberta	Note 1
<i>T. ratherfordi</i> (Russell, 1929)	Paleocene, Alberta	Note 1
" <i>Helicina</i> " <i>cretacea</i> Yen, 1954	Upper Cretaceous, Wyoming	
" <i>H.</i> " <i>cokevillensis</i> Yen, 1954	Upper Cretaceous, Wyoming	
" <i>H.</i> " <i>vokesti</i> Hanna, 1936	Eocene, California	
Family Cyclophoridae		
		Cyclophoridae (sensu lato): American tropics, Andes; E and SE Asia; Polynesia; E Africa, Malagasy Is. (Solem 1979)
<i>Paleocyclotus</i> ? sp. (Yen 1952)	Upper Cretaceous, Wyoming	
<i>Pseudarinia convexa</i> Yen, 1952	Upper Cretaceous, Wyoming	
<i>P. pupilla</i> Yen, 1952	Upper Cretaceous, Wyoming	
<i>P. uniplica</i> Yen, 1954	Upper Cretaceous, Wyoming	
<i>Rhiostoma americana</i> Hanna, 1920	Oligocene, Oregon	<i>Rhiostoma</i> : SE Asia (Wenz 1938)
Subclass Pulmonata		
Family Ellobiidae		
<i>Carychium</i> sp. (La Rocque 1960; Taylor 1975)	Eocene, Wyoming, Utah	<i>Carychium</i> : North America except NE Cordillera; American tropics; Europe, Asia, Philippines, Indonesia (Pilsbry 1948; Zilch 1959)
Family Tornatellinidae		
<i>Protornatellina isoclina</i> (White, 1895)	Upper Cretaceous, Wyoming	Tornatellinidae: Polynesia and Juan Fernandez Is. (Solem 1979)
Family Pupillidae		
<i>Gastrocopta</i> (<i>Gastrocopta</i>) sp. (Taylor 1975)	Eocene, central Wyoming	Subgenus <i>Gastrocopta</i> : South Dakota to SW U.S.; American tropics; Africa, Mascarene Is., Ceylon, Philippines (Pilsbry 1948)
<i>Pupoides</i> (<i>Ichnopupoides</i>) sp. (Taylor 1975)	Eocene, central Wyoming	<i>Ichnopupoides</i> : South Dakota to Arizona (no Montana or central Wyoming records); Mexico to Argentina, Chile (this paper)
<i>P. (I.) tephrodes</i> n. sp.	Eocene or Oligocene, Montana	
<i>P. (I.)</i> sp., cf. <i>P. (I.) hordaceus</i> (Gabb, 1866) (this paper)	Eocene or Oligocene, Montana	<i>P. (I.) hordaceus</i> : SE Wyoming to New Mexico (Bequaert and Miller 1973)
Family Strobilopsidae		
		Strobilopsidae, <i>Strobilops</i> : E North America; American tropics; E Asia (Pilsbry 1948); Baja California (Miller and Christensen 1980)

TABLE 2. CONTINUED.

Taxon	Fossil occurrence	Holocene range
<i>Strobilops</i> sp. (Taylor 1975)	Early Tertiary, Wyoming	
Family Clausiliidae		Clausiliidae: Eurasia; Andes; 2 spp. in Greater Antilles (Solem 1979)
Genus and sp. indet. (Taylor 1975)	Eocene, Wyoming	
Family Subulinidae		Subulinidae: Tropics except Polynesia and Micronesia; S Africa; Mediterranean region; high diversity in Africa and tropical South America (Zilch 1959)
<i>Pseudocolumna spitzia</i> Tozer, 1956	Upper Cretaceous, Alberta	
<i>P. vermicula</i> (Meek and Hayden, 1857)	Paleocene, North Dakota	Note 2
<i>P. haydeniana</i> (Cockerell, 1906)	Paleocene, Alberta, North Dakota; Eocene, Wyoming	Note 2
<i>P.</i> spp. (Taylor 1975)	Paleocene and Eocene, Wyoming	
Family Urocoptidae		Urocoptidae: southern U.S.; American tropics (Zilch 1960)
<i>Holospira dyeri</i> Tozer, 1956	Upper Cretaceous, Alberta	<i>Holospira</i> : Texas, New Mexico, Arizona; Mexico (Bequaert and Miller 1973)
<i>H. grangeri</i> Cockerell, 1914	Paleocene, New Mexico	Note 3
<i>H.</i> (?) sp. (La Rocque 1960; McKenna, Robinson, and Taylor 1962; Dorr 1969)	Paleocene and Eocene(?), Utah; Eocene, Wyoming	
<i>H. leidy</i> (Meek, 1873)	Eocene, Wyoming	
<i>H.</i> (?) <i>adventicia</i> Russell, 1955	Eocene or Oligocene, British Columbia	
Genus and sp. indet. (Taylor 1975)	Eocene, Montana, Wyoming	
Family Bulimulidae		Bulimulidae: In North America, only one species north of southern tier of states (Pilsbry 1946); Central and South America; Australasia
<i>Bulimulus</i> (?) sp. (La Rocque 1960)	Eocene, Utah	<i>Bulimulus</i> (sensu lato): southern U.S.; Mexico to South America (Zilch 1960)
<i>Oreoconus jepseni</i> (Russell, 1931)	Eocene, Wyoming	
<i>O. planispira</i> Taylor, 1962	Eocene, Wyoming	
<i>O.</i> spp. (Oriol 1962; Taylor 1975)	Eocene and Oligocene, Wyoming; Eocene, Utah	
Family Charopidae		Charopidae: Australia, New Zealand, New Caledonia; South Africa; Central and South America; Idaho to Arizona (Solem 1979)
aff. <i>Charopa</i> (Taylor 1975)	Paleocene, Wyoming	
Family Discidae		
<i>Anguspira russelli</i> Tozer, 1956	Paleocene, Alberta	<i>Anguspira</i> : North America, mainly S of U.S.—Canadian border; questionably, Alberta (La Rocque 1953); no Wyoming records
<i>A. holroydensis</i> Russell, 1956	Miocene, Wyoming	
Family Arionidae		

TABLE 2. CONTINUED.

Taxon	Fossil occurrence	Holocene range
<i>Binneya antiqua</i> Russell, 1955	Eocene or Oligocene, British Columbia	<i>Binneya</i> : California Channel Is.; Isla de Guadalupe, Baja California (Pilsbry 1948)
<i>Craterarion pachyostracon</i> Taylor, 1954	Miocene, southern California	<i>Craterarion</i> : possibly Holocene of central California (Taylor and Roth, MS)
Family Zonitidae		
" <i>Gastrodonta</i> " <i>coryphodontis</i> Cockerell, 1914	Eocene, Wyoming	Note 4
" <i>G.</i> " <i>imperfecta</i> Hanna, 1920	Oligocene or Miocene, Oregon	Note 4
" <i>Omphalina</i> " <i>laminarum</i> Cockerell, 1906	Oligocene, Colorado	Note 4
" <i>O.</i> " <i>oreodontis</i> Cockerell and Henderson, 1912	Oligocene, Colorado	Note 4
<i>Ventrudens</i> (?) <i>lens</i> (Gabb, 1864)	Upper Cretaceous, California	Note 5. <i>Ventrudens</i> : E North America (Pilsbry 1946)
<i>V.</i> (?) sp. (Russell 1955)	Eocene or Oligocene, British Columbia	
Family Polygyridae		
<i>Polygyra</i> (?) <i>petrochlora</i> Cockerell, 1914	Eocene, New Mexico	<i>Polygyra</i> (including <i>Daedalochila</i>): SE North America, Mexico, Antilles, Bermuda (Pilsbry 1940)
<i>P.</i> (?) sp. (Taylor 1975)	Eocene, Wyoming	
" <i>P.</i> " <i>veternior</i> (Cockerell, 1915)	Eocene, Wyoming	
" <i>P.</i> " <i>expansa</i> Hanna, 1920	Oligocene or Miocene, Oregon	Note 6
" <i>P.</i> " <i>martini</i> Hanna, 1920	Oligocene or Miocene, Oregon	Note 6
<i>Triudopsis</i> (?) spp. (Taylor 1975)	Eocene and Oligocene, Wyoming	<i>Triudopsis</i> : Washington, Oregon, Idaho; E and midwestern U.S. (Vagvolgyi 1968)
<i>Vespericola</i> (?) <i>dalli</i> (Stearns, 1885)	Oligocene or Miocene, central Oregon	<i>Vespericola</i> : Alaska to California; in Oregon, west of Cascade crest (Pilsbry 1940)
Family Oleacinidae		
Genus and sp. indet. (Taylor 1975)	Eocene, Wyoming	Oleacinidae: SE North America to Texas; American tropics; Mediterranean region (Pilsbry 1948; Zilch 1960)
Family Camaenidae		
<i>Caracolus aquilonaris</i> Bishop, 1979	Oligocene, Nebraska	<i>Caracolus</i> : Greater Antilles (Bishop 1979)
<i>Hodopoeus crassus</i> Pilsbry and Cockerell, 1945	Paleocen(?) SW U.S.	Note 7
<i>H. hesperarche</i> (Cockerell, 1914)	Paleocen(?), Texas	Note 7
<i>Kanabohelix kanabensis</i> (White, 1876)	Upper Cretaceous, Utah	Note 8
<i>Pleurodonte</i> (<i>Pleurodonte</i>) <i>wilsoni</i> Roth, 1984	Eocene and Oligocene, W Texas	Subgenus <i>Pleurodonte</i> : Lesser Antilles (Roth 1984)
<i>P.</i> (<i>Dentellaria</i>) (?) sp. (Roth 1984)	Eocene, W Texas	Subgenus <i>Dentellaria</i> : Jamaica (Roth 1984)
" <i>Helix</i> " <i>spatiosa</i> Meek and Hayden, 1861	Paleocene, Alberta, North Dakota; Paleocene and Eocene, Wyoming; Eocene, Texas	Note 9
" <i>Oreohelix</i> " <i>steimi</i> Cockerell, 1914	Paleocene, New Mexico	Note 9
Genus and sp. indet. (Roth 1984)	Eocene, W Texas	

TABLE 2. CONTINUED.

Taxon	Fossil occurrence	Holocene range
Family Ammonitellidae		
<i>Ammonitella lunata</i> (Conrad, 1871)	Oligocene or Miocene, Oregon	<i>Ammonitella</i> : Sierra Nevada, California (Pilsbry 1939)
<i>Polygyrella amplexa</i> (Meek and Hayden, 1857)	Upper Cretaceous, Montana	<i>Polygyrella</i> : NE Oregon to W Montana (Pilsbry 1939)
<i>P. parvula</i> (Whiteaves, 1885)	Upper Cretaceous, Alberta	
<i>P. venerabilis</i> (Russell, 1937)	Upper Cretaceous, Alberta	
<i>P. sp.</i> , cf. <i>P. polygyrella</i> (this paper)	Eocene, Montana	
<i>P. sp.</i> (Ross 1959; Taylor 1975)	Eocene, Montana, Wyoming	
<i>P. polygyrella</i> (Bland and Cooper, 1861)	Oligocene or Miocene, central Oregon	<i>P. polygyrella</i> : NE Oregon to W Montana (Pilsbry 1939)
Family Oreohelicidae		
<i>Radiocentrum</i> (?) <i>anguliferum</i> (Whiteaves, 1885)	Upper Cretaceous, Alberta	<i>Radiocentrum</i> : SW U.S. and N Mexico; Baja California Sur (this paper)
<i>R. thurstoni</i> (Russell, 1926)	Paleocene, Alberta	
<i>R. grangeri</i> (Cockerell and Henderson, 1912)	Eocene, Wyoming	
<i>R. laeviformis</i> n. sp.	Eocene(?), Montana	
<i>R. taylori</i> n. sp.	Eocene or Oligocene, Montana	
<i>R. hendersoni</i> (Russell, 1938)	Oligocene, Colorado	
Family Helminthoglyptidae		
		Helminthoglyptidae: Alaska to California; SW U.S.; Mexico, Central America, Florida Keys, Antilles; Andes from Ecuador to W Argentina (Pilsbry 1939)
<i>Glyptertes rotundatus</i> (Russell, 1931)	Paleocene, Alberta	
<i>G. veternis</i> (Meek and Hayden, 1861)	Eocene, Wyoming	
<i>Helminthoglypta bozemanensis</i> n. sp.	Eocene or Oligocene, Montana	<i>Helminthoglypta</i> : S Oregon to N Baja California (this paper)
<i>H.</i> (?) <i>sp.</i> (Taylor 1975)	Oligocene, Wyoming	
<i>Hemitrochus</i> (?) <i>sp.</i> (Taylor 1975)	Oligocene, Wyoming	<i>Hemitrochus</i> : S Florida, Antilles (Turner 1958)
<i>Lysinoe breedlovei</i> Roth, 1984	Eocene and Oligocene, W Texas	<i>Lysinoe</i> : Chiapas, Mexico; Central America (Roth 1984)
<i>Mesoglyptertes sagensis</i> Yen, 1952	Upper Cretaceous, Wyoming	
<i>Monadenia antecessens</i> (Stearns, 1900)	Oligocene or Miocene, central Oregon	<i>Monadenia</i> : Alaska to California; in Oregon, W of Cascade crest (Roth 1981b)
<i>M. dubiosa</i> (Stearns, 1902)	Oligocene or Miocene, central Oregon	
<i>M. (Shastelix?) marginicola</i> (Conrad, 1871)	Oligocene or Miocene, central Oregon	<i>Shastelix</i> : Klamath Mountains, N California (Roth 1981b)
<i>Polymita texana</i> Roth, 1984	Eocene, W Texas	<i>Polymita</i> : Oriente Province, Cuba (Zilch 1960)
<i>Xerarionta waltmilleri</i> Roth, 1984	Oligocene, W Texas	<i>Xerarionta</i> : S California to Baja California (Roth 1984)
" <i>Helix</i> " <i>adapis</i> White, 1886	Paleocene, New Mexico	Note 10
" <i>H.</i> " <i>nacimientensis</i> White, 1886	Paleocene, New Mexico	Note 10
Undescribed genus and sp. (Taylor 1975)	Eocene, Wyoming	

Notes

1. Solem (1979) suggested relationship to West Indian Camaenidae; now shown to belong to one (Bishop 1980) or more (Solem in press) genera of Heliciniidae.

tions and faunal replacements in many groups of organisms beyond that evident in the first two-thirds of the Eocene. Continental aridity increased in interior regions of North America and general world-wide climatic equability decreased" (Lillegraven 1979:344). Axelrod (1981, table 1) noted that the period around 40 million years before present was one of spreading dry climate in southwestern North America.

As a generalization (admittedly much simplified), organisms in the western interior of North America that were most sensitive to cooling temperatures should have undergone southward displacement: the general trend of isotherms is latitudinal. Organisms most sensitive to drought (annual or seasonal) should have been displaced to east or west: away from the complex topography of the Great Basin and Rocky Mountains, the general trend of isohyets is longitudinal (U.S. Dept. Commerce 1968). What one in fact sees is a mixture of displacements, both among Bozeman Group taxa and among North American land mollusk groups in general (Table 2).

At the family level, the late Eocene and early Oligocene was the time of greatest modernization of the worldwide land mammal fauna, archaic kinds generally adapted to warmer climates giving way to modern varieties more tolerant of the temperate climate of the late Cenozoic (Lillegraven 1979). For North American land mollusks, at least, the time seems not to have been one of evolutionary innovation so much as local extinction and biogeographic rearrangement.

ACKNOWLEDGMENTS

I am indebted to Dwight W. Taylor for introducing me to the mollusk fauna of the Bozeman Group and for a critical reading of the manu-

script. I am also grateful to John H. Hanley for lending material from the U.S. Geological Survey collections, to Glenn Goodfriend for his suggestions on the generic allocation of certain fossil species, to Emmett Evanoff for advice on stratigraphic nomenclature, and to Alan Solem for a preprint of his work in press. Scanning electron microscope photographs were taken in the SEM facility of the Department of Entomology, CAS; I thank Mary Ann Tenorio for her competent instruction and assistance.

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2. These *Pseudocolumna* "can be interpreted as smooth-shelled bulimulids equivalent in shape and size to South American *Bostryx* (*Peroneus*) rather than to any African subulinids" (Solem 1979:281).

3. The Paleocene *Holospira* sites in New Mexico are about 370 km north of the modern range of the genus (Bequaert and Miller 1973).

4. Genus of original proposal almost certainly incorrect; allocation uncertain, possibly helicoid (Pilsbry 1946; Solem 1979).

5. Pilsbry (in Stewart 1926) assigned this species to *Ventridens* but later (1946:436) expressed reservations about the assignment.

6. "Not . . . certainly referable to any recent West Coast genera of Polygyridae" (Pilsbry 1940:893).

7. Solem (1978, 1979) noted resemblance between *Hodopoeus* and the extant South American camaenid genus *Isomeria*.

8. Regarded as helicid by Bishop (1980) but shown by Solem (in press) to be stylommatophoran; possibly camaenid (Solem 1978, 1979).

9. New genus of Camaenidae (D. W. Taylor, personal communication). Related Paleogene species occur in New Mexico and southern California.

10. Allocation uncertain, possibly helminthoglyptid (Solem 1979, *H. adapis*; Taylor 1975, *H. nactimentensis*).

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